Ailsacrinus gen. nov., an aberrant millericrinid from the Middle Jurassic of Britain

P. D. Taylor

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The genus *Ailsacrinus* is proposed for the millericrinids *A. abbreviatus* sp. nov., from a new Lower–Middle Bathonian locality at Eastington, near Northleach (Gloucestershire), and the established U. Bathonian species *A. prattii* (Gray 1828), known mainly from Lansdown Hill, north of Bath. *Ailsacrinus* is unusual in having a short tapering column, highly variable in length (1–70 columnals), with a rounded distal end. The small calyx contains reduced basals and, in some individuals, an irregular development of accessory plates often with tubercles. Previously undescribed among millericrinids are syzygies in the arms of *Ailsacrinus*, and differentiation of pinnules into an oral series with transversely-ridged pinnulars and a distal series with cover plates. Well-preserved stereom ultrastructure is described in *A. abbreviatus*. The palaeoecology of *Ailsacrinus* is inferred using functional morphological analysis, comparison with living echinoderms, preservational evidence, and facies relationships. Following detachment of the proximal part of the column and crown from the substratum – perhaps quite late in ontogeny – individuals of *Ailsacrinus* probably led a free-living existence. There is some evidence for columnal addition after detachment in *A. abbreviatus*, although not in *A. prattii*, and columnals may have been shed occasionally. Eleutherozoic adults of *A. abbreviatus* seem to have lived in dense interlocking aggregations or mats which would have provided individuals with stability in the absence of grasping cirri, and might also have acted as current baffles to aid suspension feeding. The well-articulated Eastington crinoids were apparently buried catastrophically by shell sand. Although *Ailsacrinus* is presumed to have evolved from an attached millericrinid, the evolutionary trend within the genus is in the opposite direction. Morphological similarities with comatulids may be due to synplesiomorphy or convergence.

Introduction

In 1882 P. Herbert Carpenter published the first full description of the 'Lansdown Encrinite', *Millericrinus prattii* (Gray 1828), an unusual crinoid characterized by a short tapering stem without any obvious means of attachment. Several later authors (Bather 1900, Kirk 1911, Gislén 1934, Ubaghs *et al.* 1978, Roux 1978) used Carpenter's description and reproduced his figures when discussing *M. prattii* as an example of a free-living (eleutherozoic) crinoid belonging to a group otherwise consisting of permanently attached crinoids. It is somewhat surprising, then, that this interesting crinoid has not been re-studied since the time of Carpenter.

Most museum specimens of *M. prattii* were obtained from the Great Oolite of Lansdown Hill, near Bath. However, Carpenter also mentioned apparently conspecific crinoids from North-leach, about 60 km north-east of Bath (Fig. 1). A re-examination of this crinoid was prompted by the discovery of a locality near Northleach which has yielded several hundred well-preserved individuals from rocks of an earlier age than those present at Lansdown. During the study it became apparent that the Northleach and Lansdown crinoids were not conspecific. However, they proved to be sufficiently similar to one another and distinct from established millericrinid genera to warrant their inclusion in a new genus. *Ailsacrinus* gen. nov. is proposed to include the type-species *A. abbreviatus* sp. nov., from Northleach, and *A. prattii* (Gray).

Detailed morphological study of *Ailsacrinus*, as well as corroborating many of Carpenter's observations, has revealed new information relating to arm and pinnule structure and stereom ultrastructure. This has enabled the ontogeny, palaeoecology and phylogenetic affinities of *Ailsacrinus* to be reconsidered.

Specimens studied are in the collections of the British Museum (Natural History) (abbreviated BMNH), the Sedgwick Museum, Cambridge (SM), and the Oxford University Museum (OUM).

Localities

Ailsacrinus abbreviatus

NORTHLEACH AND EASTINGTON. Carpenter (1882) was the first to note the occurrence of the crinoid herein called *A. abbreviatus* in the 'Stonesfield Slate' of Northleach, Gloucestershire. He referred to specimens in the British Museum (Natural History), apparently register numbers 9570, 9572 and 9574 of the Mantell Collection. Other BMNH specimens from Northleach are in

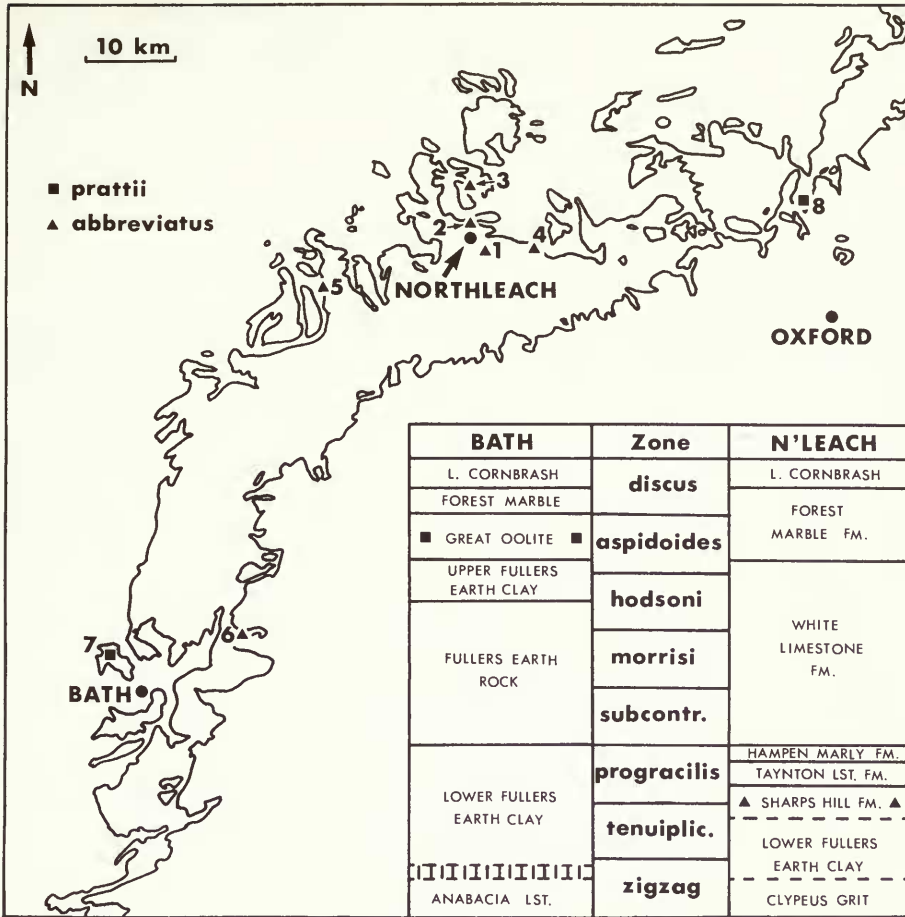| BATH	Zone	N'LEACH
L. CORNBRASH	discus	L. CORNBRASH
FOREST MARBLE	discus	FOREST MARBLE FM.
■ GREAT OOLITE ■	aspidoides	FOREST MARBLE FM.
UPPER FULLERS EARTH CLAY	hodsoni	WHITE LIMESTONE FM.
FULLERS EARTH ROCK	morrisi	WHITE LIMESTONE FM.
FULLERS EARTH ROCK	subcontr.	WHITE LIMESTONE FM.
LOWER FULLERS EARTH CLAY	progracilis	HAMPEN MARLY FM. / TAYNTON LST. FM. / ▲ SHARPS HILL FM. ▲
LOWER FULLERS EARTH CLAY	tenuiplic.	LOWER FULLERS EARTH CLAY
ANABACIA LST.	zigzag	CLYPEUS GRIT

Fig. 1   Geographical and stratigraphical occurrence of *Ailsacrinus* gen. nov. in southern England. Map shows Bathonian outcrop together with localities for *A. abbreviatus* sp. nov. (triangles numbered 1–6) and *A. prattii* (Gray) (squares numbered 7 and 8). Locality details: 1, new locality near Eastington; 2, Isolation Hospital, Northleach; 3, Notgrove; 4, Windrush; 5, Miserden Park; 6, Corsham; 7, Lansdown Hill; 8, Kirtlington. Stratigraphical details based on Cope *et al.* (1980) modified for Northleach.

the Richardson Collection (E14882–5) and are labelled 'Lower Great Oolite, Quarry near Isolation Hospital'. This is presumably the old quarry described by Richardson (1933: 42) and located north of the town (loc. 2 of Fig. 1).

The newly-discovered locality is a small exposure on a low river cliff near Eastington, 2 km south-east of Northleach (loc. 1 of Fig. 1). Precise locality details have been lodged with the Nature Conservancy Council. Facies comparisons and local geological mapping suggest that the limestone exposed here lies within the Sharps Hill Formation (Sellwood & McKerrow 1974) and its age is likely to be either early Bathonian *tenuiplicatus* Zone or mid-Bathonian *progracilis* Zone (Cope *et al.* 1980). An alternative possibility is that the crinoid bed belongs to the Taynton Limestone Formation (*progracilis* Zone) which is of a similar facies to the Sharps Hill Formation around Northleach. However, this seems less likely because the Taynton Limestone Formation is quartz-deficient, whereas the crinoid bed abounds in quartz. Crinoids occur throughout the thickness (about 26 cm) of the crinoid bed but are most conspicuous on several successive bedding planes (Fig. 2) and tend to be more abundant and better preserved near to the base of the bed. The bed overlies and grades into an oobiosparite and in turn is overlain, with a sharp

Fig. 2 *Ailsacrinus abbreviatus* gen. et sp. nov. covering a bedding plane from the Eastington crinoid bed (Bathonian, ? Sharps Hill Fm.), BMNH E67791. Most of the crinoids on this undersurface are upright but some are prostrate or obliquely orientated. Divisions of scale bar are 1 cm.
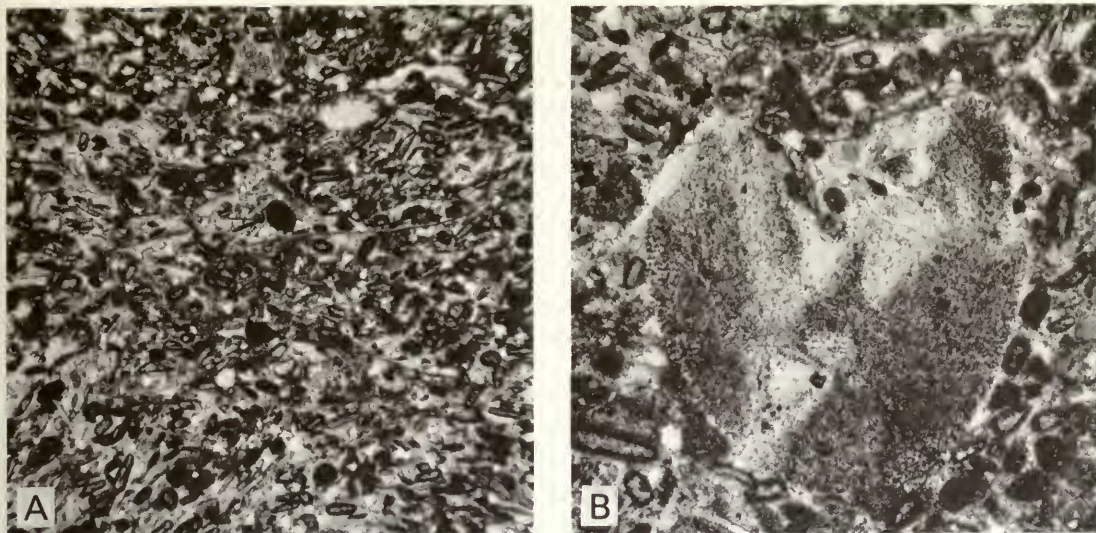
Fig. 3 Thin section cut from the Eastington Crinoid Bed, BMNH E67832. A, sandy bio-oosparite composed mostly of molluscan shell fragments subparallel to bedding; PPL, ×17. B, brachial of *Ailsacrinus abbreviatus* gen. et sp. nov.; PPL, ×33.

contact, by a cross-bedded shelly limestone. Lithologically, the crinoid bed is a grain-supported (grainstone), sandy bio-oosparite composed largely of molluscan shell fragments, 0·1–0·4 mm in length, which are generally orientated parallel to the bedding (Fig. 3). Isolated crinoid ossicles are scarce. Subrounded to subangular quartz grains make up about 20% of the rock and impart a sandy texture to weathered surfaces. Development of the fossils is aided by the presence of thin layers or drapes of clay which are easily washed away from the crinoid-covered bedding planes. The clay contains illite, quartz and calcite (determined by X-ray diffractometry). Good preservation of stereom ultrastructure at this locality is probably the result of clay particles penetrating the outer part of the skeleton and preventing the formation of syntaxial overgrowths within the porous lattice. Apart from the crinoids, macrofossils are sparse and poorly preserved; a few abraded brachiopods, epifaunal bivalves and echinoids are present, together with woody carbonaceous fragments. Preservation of the crinoids is discussed below under Palaeoecology, p. 65.

OTHER LOCALITIES. Richardson (1904: pl. 19, fig. 1) illustrated crowns of *A. abbreviatus* supposedly from the U. Aalenian (*murchisonae* Zone) Lower Limestone of Andoversford, 10 km west of Northleach. These specimens were not from his personal collection and their stratigraphical horizon and provenance may be doubted.

The J. Morris Collection at the BMNH contains a specimen (E67) labelled 'Great Oolite, Corsham, Wiltshire', loc. 6 of Fig. 1.

Carpenter (1882) mentions the occurrence of *M. prattii*, probably referring to *A. abbreviatus*, at Windrush (loc. 4 of Fig. 1), Notgrove (loc. 3) and Miserden Park (loc. 5). Material from Miserden Park includes BMNH E14661 figured in Carpenter's pl. 1, fig. 9. No exact stratigraphical details are given but all may be from low in the Bathonian sequence.

Ailsacrinus prattii

LANSDOWN. The great majority of existing *A. prattii* specimens were obtained over 150 years ago from Lansdown Hill near Bath (loc. 7 of Fig. 1). As early as 1833 Jelly wrote of the small chance of ever procuring further specimens. Lansdown Hill is now part of urban Bath. Initially, Gray (1828) made the mistake of supposing the Lansdown crinoids to have come from the Lias but Jelly corrected this misapprehension and gave their horizon as Great Oolite. A well record

from Beckford's Tower at the summit of Lansdown Hill records 30 feet of Great Oolite (Woodward 1894: 243) which, around Bath, is generally regarded as being of late Bathonian *aspidoides* Zone age (Cope *et al.* 1980). The Lansdown crinoids are contained in a matrix of coarse oobiosparite. They are reasonably well articulated but arms are often separated from stem and calyx. Most are preserved in a prostrate attitude, i.e. with the stem lying parallel to bedding. An associated fauna includes well-preserved echinoids. Both Jelly (1833) and Carpenter (1882) mention the occurrence of *Pentacrinites* in association with *A. prattii*. The Sedgwick Museum (Cambridge) collections contain two pieces (J33842, J33850) with isocrinids but these are in a finer-grained rock and are without associated *A. prattii*.

KIRTLINGTON. A single specimen (J14219) in the Oxford University Museum is allegedly from the Great Oolite of Kirtlington (loc. 8 of Fig. 1). This is also likely to be of late Bathonian age and the matrix suggests (T. J. Palmer, personal communication 1979) that it may be from the Lower Cornbrash (*discus* Zone).

Systematic descriptions

Order **MILLERICRINIDA** Sieverts-Doreck *in* Moore *et al.*, 1952
Suborder **MILLERICRININA** Sieverts-Doreck in Moore *et al.*, 1952
Family **MILLERICRINIDAE** Jaekel, 1918
Genus *AILSACRINUS* nov.

DIAGNOSIS. Millericrinidae with reduced column, tapering distally and terminated by a rounded columnal; incomplete or lenticular columnals may be present; cup bowl-shaped to conical with small basals and often with irregularly developed, tiny accessory plates, interbasally-placed, generally tuberculate; arms have frequent syzygies; pinnules differentiated into oral and distal series, the oral pinnules having high pinnulars with adoral transverse ridges.

TYPE SPECIES. *Ailsacrinus abbreviatus* sp. nov., Lower–Middle Bathonian (M. Jurassic), Gloucestershire, England. This species is chosen in preference to *A. prattii* because of the superior preservation of available material.

REMARKS. This new genus is proposed to accommodate two aberrant millericrinid species in which the reduced stem with a rounded end is a synapomorphy. They are also distinguished from previously-described millericrinids by having differentiated oral pinnules and abundant syzygies in the arms.
   The established species now referred to *Ailsacrinus*, *Encrinites* (*Apiocrinites*) *prattii* Gray 1828, has usually been placed in the genus *Millericrinus* d'Orbigny, 1841. However, *Millericrinus*, as defined by the type species *Encrinites milleri* von Schlotheim 1823, has a flat-bottomed, five-sided cup with large basals and a stem which does not increase in diameter towards the cup (see Rasmussen *in* Ubaghs *et al.* 1978: fig. 550,1; Roux 1978: fig. 9). *E. prattii* was provisionally included by Rasmussen (*in* Ubaghs *et al.* 1978: T822) in the genus *Liliocrinus* Rollier, 1911, the type species of which was designated by the same authors as *Millericrinus polydactylus* d'Orbigny 1841. In this species the basals and radials are of approximately equal size and the arms divide two or three times, unlike *Ailsacrinus* in which the basals are considerably smaller than the radials and there is only one division of the arms.

NAME. *Ailsacrinus* is named in recognition of Miss Ailsa M. Clark of the Department of Zoology, British Museum (Natural History).

Ailsacrinus abbreviatus sp. nov.

1882 *Millericrinus Prattii* Gray; Carpenter: 29 (*partim*); pl. 1, fig. 9 only.
1904 *Millericrinus Pratti* Gray; Richardson: 250; pl. 19, fig. 1.

DIAGNOSIS. A species of *Ailsacrinus* with small, bowl-shaped cup and tiny triangular basals which either fail to touch or barely touch adjacent basals; radials high relative to basals; accessory plates inconspicuous; column tapering distally and short (1–9 columnals); distal facet of proximale with petaloid areola.

HOLOTYPE. BMNH E67797 (Fig. 25, p. 52), Bathonian (?Sharps Hill Fm.), Eastington, Gloucestershire. P. D. Taylor Coll., 1979.

PARATYPES. BMNH 9570, 9572, 9574, Stonesfield Slate, Northleach; Mantell Coll., 1839. E67, Great Oolite, Corsham, Wiltshire; J. Morris Coll., 1880. E14661 (Carpenter 1882: pl. 1, fig. 9), Forest Marble?, Miserden, Gloucestershire; J. F. Walker Coll., 1908. E14882–5, Lower Great Oolite, Quarry near Isolation Hospital, Northleach; L. Richardson Coll., 1910. E67791–6, E67798–889 and E68070–84, Bathonian (?Sharps Hill Fm.), Eastington, Gloucestershire; P. D. Taylor Coll., 1979.

OCCURRENCE. Lower–Middle Bathonian of Gloucestershire (Fig. 1). The only accurate stratigraphical information available is from Eastington where the rocks exposed are probably of the Sharps Hill Formation, regarded as late early Bathonian (*tenuiplicatus* Zone) or early mid-Bathonian (*progracilis* Zone) in age.

DESCRIPTION. Details of the morphology of *A. abbreviatus* and *A. prattii* are considered together below, p. 45.

REMARKS. This new species has been previously included in *A. prattii* (Carpenter 1882, Richardson 1904). However, these smaller crinoids from the Lower–Middle Bathonian can be distinguished consistently from topotypes of *A. prattii* which occur higher in the Bathonian at Lansdown. The stem of *A. abbreviatus* is less variable and there are none having stems with more than 10 columnals. The cup is smaller and more bowl-shaped than in *A. prattii*, basals are smaller, and accessory plates are less conspicuous, never exceeding one per ray.

NAME. The trivial name *abbreviatus* alludes to the greatly reduced basals and stem in this species.

Ailsacrinus prattii (Gray 1828)

	1828	*Encrinites* (*Apiocrinites*) *Prattii* Gray: 219.
	1831	*Apiocrinites obconicus* Goldfuss: 187; pl. 57, figs 5a–n.
	1833	*A.* [*Apiocrinites*] *fusiformis* Jelly: 46; pl. 1, figs 1–11.
	1840	*Millericrinus obconicus* (d'Orb.) [*sic*] d'Orbigny: 80; pl. 14, figs 23–28.
	1862	*Apiocrinites obconicus* nobis [*sic*]; Goldfuss: 174; pl. 57, figs 5a–n.
non	1881	*Millericrinus obconicus* d'Orb.–*Apiocrinites obconicus* Goldf.; Morière: 85; pl. 1 (= *Millericrinus morierei* de Loriol 1883).
	1882	*Millericrinus Prattii* (Gray) Carpenter: 29 (*partim*); pl. 1, figs 1–8, 10–23 (fig. 9 = *Ailsacrinus abbreviatus* sp. nov.).
	1884	*Millericrinus Prattii* (Gray); de Loriol: 618.
	1900	*Millericrinus pratti* (Gray); Bather: 135; fig. 52.
	1911	*Millericrinus prattii* (Gray); Kirk: 48; pl. 6, figs 1–6.
	1934	*Millericrinus prattii* (Gray); Gislén: 6, fig. 7.
	1936	*Millericrinus pratti* (Gray); Biese: 464.
	1978	*Millericrinus prattii* (Gray); Ubaghs *in* Ubaghs *et al.*: T93; fig. 70,2.
	1978	*Liliocrinus prattii* (Gray): Rasmussen *in* Ubaghs *et al.*: T822; fig. 551,2a, b, f, g, i, l.

REVISED DIAGNOSIS. A species of *Ailsacrinus* with moderately large, bowl-shaped to conical cup; basals touching adjacent basals and pentagonal in shape; radials similar in height to basals; accessory plates generally conspicuous, frequently more than one per ray; column tapering distally and of highly variable length (one to more than 66 columnals); distal facet of proximale with tuberculate areola, not petaloid.

HOLOTYPE. The single specimen (Fig. 4) described by Gray (1828), BMNH E24663; Great Oolite (probably Upper Bathonian *aspidoides* Zone), Lansdown, near Bath.

3*

Fig. 4   *Ailsacrinus prattii* (Gray). **Holotype** BMNH E24663, from the Great Oolite of Lansdown Hill;
×2.

OTHER MATERIAL. BMNH: 48900, Lansdown; R. Etheridge Coll., 1868. E5722, Great Oolite, Lansdown. E24664, Great Oolite, ?locality; Bowerbank Coll., 1865. OUM: J14219, Great Oolite, Kirtlington. SM: J33689–734, J33769–70, J33806–15, J33822, J33834, Great Oolite, Lansdown; Walton Coll.

DESCRIPTION. See below.

REMARKS. The synonymy lists only those references which give descriptions or figures of *A. prattii*. Elsewhere, the species has been cited as an example of an eleutherozoic crinoid or included in stratigraphical lists of fossils. Pre-1936 references of this type are given by Biese (1936).

Apiocrinites obconicus was described by Goldfuss (1831) using specimens obtained from the Great Oolite of Bath. The illustrations of Goldfuss show that these are clearly conspecific with the earlier *Encrinites prattii* of Gray. D'Orbigny (1840) acknowledged Goldfuss' species but appended his own name as author when referring the species to *Millericrinus*. Crinoids from the Bathonian of Normandy, considered to be the same species by Morière (1881), were later described as *Millericrinus morierei* by de Loriol (1883). They differ from *A. prattii* in having long stems and a more conical, *Apiocrinites*-like transition between stem and cup.

Jelly (1833) was aware that the Lansdown species had been named *Encrinites prattii* by Gray (1828) but, being critical of Gray because he had stated incorrectly that their horizon was Lias and also employed a specific name derived from a proper name, chose to ignore this name. Instead, he called the crinoid the 'Lansdown Encrinite' throughout most of his paper before, in a concluding paragraph (p. 46) stating ' . . . this, perhaps, might not incorrectly be called *A.* [*Apiocrinites*] *fusiformis*'.

Knowledge of *Ailsacrinus prattii* (Gray) derives largely from the description and figures of Carpenter (1882). Although these are based mostly on Lansdown material, one of Carpenter's figures (pl. 1, fig. 9) is a specimen (BMNH E14661) from Miserden and is here considered to be *A. abbreviatus* sp. nov. Bather (1900), Kirk (1911), Gislén (1934) and Ubaghs *et al.* (1978) all copied, directly or indirectly, Carpenter's figures.

Figs 5–8 *Ailsacrinus prattii* (Gray), Great Oolite, Lansdown Hill. Specimens coated with ammonium chloride. Fig. 5, BMNH E5722, crown and proximal columnals of a presumed long-stemmed individual; ×3·5. Fig. 6, SM J33704, crinoid with a stem composed of a single rounded columnal attached to the basals; ×7. Fig. 7, SM J33700, crinoid with a short conical stem and several accessory plates in the cup; ×6. Fig. 8, SM J33719, short-stemmed crinoid with irregular lenticular columnals; ×4.

Morphology

Stem

The feature of *Ailsacrinus* which has attracted most attention is the short, variable stem tapering distally towards a rounded terminal columnal.

Carpenter (1882) emphasized the extreme variability in length of the stem among individuals of *A. prattii* from Lansdown. The longest-stemmed Lansdown crinoid has an incomplete stem of

66 columnals totalling more than 50 mm in length (Carpenter 1882: pl. 1, fig. 14). In contrast, the incomplete stem of another crinoid (pl. 1, fig. 6), although only 27 mm long, possesses 58 columnals. At the other extreme is an individual (SM J33704; pl. 1, fig. 18) with a stem composed of a single, gently convex columnal (Fig. 6). Were it not for the lack of cirri this plate would be virtually indistinguishable from a comatulid centrodorsal. Three other specimens (SM J33709, J33712 and J33715) also appear to have stems of one columnal only although these are higher than that of J33704. Two individuals have stems of two columnals only and ten others have numbers between 4 and 53; see caption to Fig. 9.

The mean value of stem length in these crinoids is equivalent to 12·5 columnals, though this figure may be an underestimate of the true population mean because the stems of crinoids with short stems are more likely to be preserved unbroken. The distribution is very strongly positively skewed with a mode of 1 columnal per stem.

The stem of *A. abbreviatus* is generally shorter than *A. prattii* and there is less variability. Fig. 9 shows the frequency of stems of different length. Again, the mean value of 4·2 columnals may be an underestimate of the true mean for the same reasons as for *A. prattii*. The longest stems consist of 9 columnals, the shortest 1 columnal (Fig. 11), and the modal value for the sample is 2 columnals. The longest stems are about 11 mm long, whereas 3 mm is a typical length.
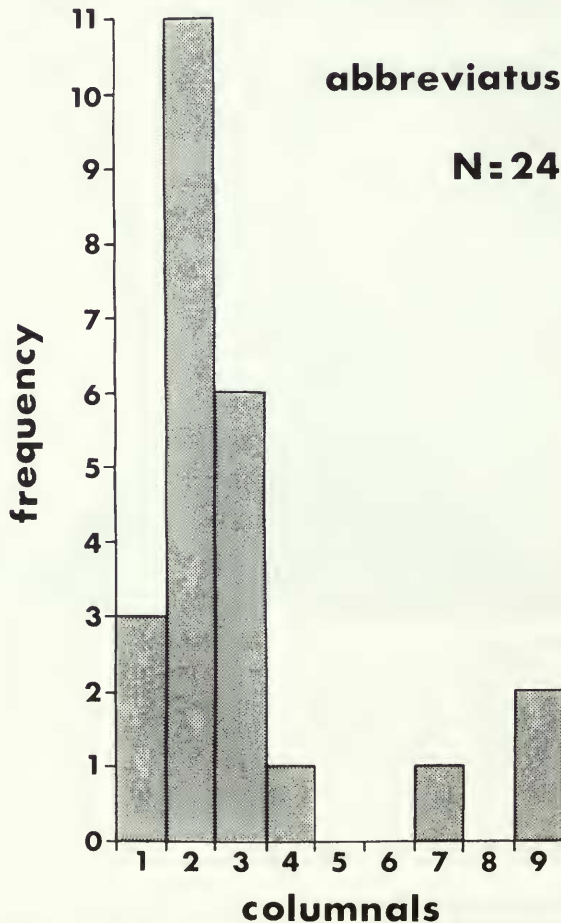
Fig. 9   Size frequency histogram of stem length (expressed as number of columnals) in 24 individuals of *Ailsacrinus abbreviatus* gen. et sp. nov. from Eastington. In contrast, 16 individuals of *A. prattii* (Gray) from Lansdown Hill showed the following numbers of columnals: 1 (4 individuals); 2 (2 individuals); 4, 5, 6, 7, 14, 17, 21, 32, 33, 53 (1 individual each).

Proximal columnals in *Ailsacrinus* have a greater diameter than distal ones, the stem tapering away from the cup. The angle of taper tends to be greater in stems with fewer columnals, for example compare Figs 7 and 20A. The proximal–distal gradient of decreasing columnal width is quantified for two long-stemmed individuals of *A. prattii* in Fig. 43 (p. 62) and is discussed below under Ontogeny (p. 58).

The most distal columnal in the majority of *Ailsacrinus* specimens has a smooth rounded end (Figs 6, 8, 11). In some cases the axial lumen is exposed but in others it appears to be plugged, as in some isocrinids (Ubaghs *et al.* 1978: T848). Certain specimens of *A. abbreviatus* have a distal columnal which, rather than being rounded, exhibits a corroded petaloid crenularium of a symplectial articulation facet (Figs 13, 14). Though observed in somewhat weathered material, this may well have been the condition of the columnal in the living crinoid prior to burial. No individuals are known with massive encrusting holdfasts, so typical of millericrinids, or the cirri which typify many other articulates. A small branching structure resembling a stem with some columnal fusion occurs on a slab (SM J33693) with arms of *A. prattii* and is depicted by Carpenter (1882: pl. 1, fig. 5). This was interpreted by both Jelly (1833) and Carpenter (1882) as a possible 'root' but unfortunately is incompletely preserved and a teratological origin cannot be discounted.

The stem of *Ailsacrinus* is homomorphic; nodals are not detectable on the basis of columnal size. Long-stemmed individuals of *A. prattii* do, however, exhibit a proximal–distal gradient of changing columnal height. Usually columnals decrease in height away from the cup but in one specimen (SM J33694) the reverse holds true (Fig. 42, p. 61).

Incomplete or 'lenticular' (Carpenter 1882) columnals are fairly common in both *A. prattii* and *A. abbreviatus*. These fail to encompass the entire circumference of the stem (Figs 8, 10, 20A). When traced around the stem they 'pinch-out' or boudinage and the space they would have occupied is taken up by thickening of the two contiguous columnals.

A single specimen of *A. prattii* (SM J33707) has an unusual overgrowth extending downwards from the cup to cover the top of the stem (Carpenter 1882: pl. 1, fig. 21). This irregular structure consists of two columnal-like plates, one of which is incomplete.

Poorly-preserved stereom on the outer surface of *A. abbreviatus* columnals appears labyrinthic in form with a spacing of 5–10 μm between elements of the lattice.

Articulations between columnals are symplectial. Externally, the crenellae and culmina are seen to interlock in a crenulate manner (Fig. 10). The distal facet of the top columnal in *A. abbreviatus* has a petaloid areola and a quinquelobate lumen (Fig. 14). In *A. prattii* the crenularium has crenellae and culmina which are better defined, and the areola is not petaloid

10   **11**

Figs 10–11 Scanning electron micrographs of the stem in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 10, BMNH E68070, part of a long stem showing crenulate symplectial articulations and a small lenticular columnal; × 11. Fig. 11, BMNH E68071, short stem composed of a rounded columnal corroded in appearance; × 5·5.
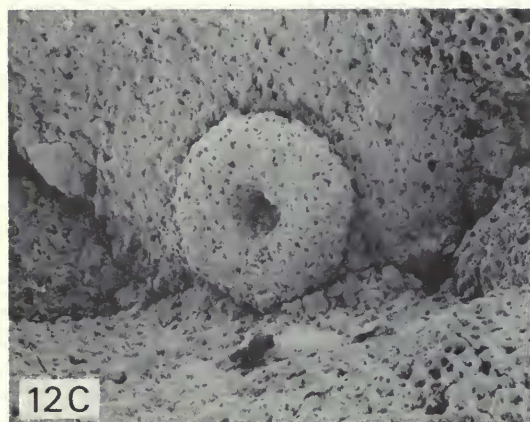
Figs 12–15   Scanning electron micrographs of the cup in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 12, BMNH E68072: A, aboral view showing broken stem, small basals and radials; × 3·7; B, tuberculate accessory plate located between basals; × 15·7; C, detail of tubercle; × 83. Fig. 13, BMNH E68073, cup with a solitary columnal attached; × 4·9. Fig. 14, BMNH E68074, corroded petaloid crenularium and axial lumen of top stem columnal; × 7. Fig. 15, BMNH E68075, stemless specimen showing basal facets; × 9·1.
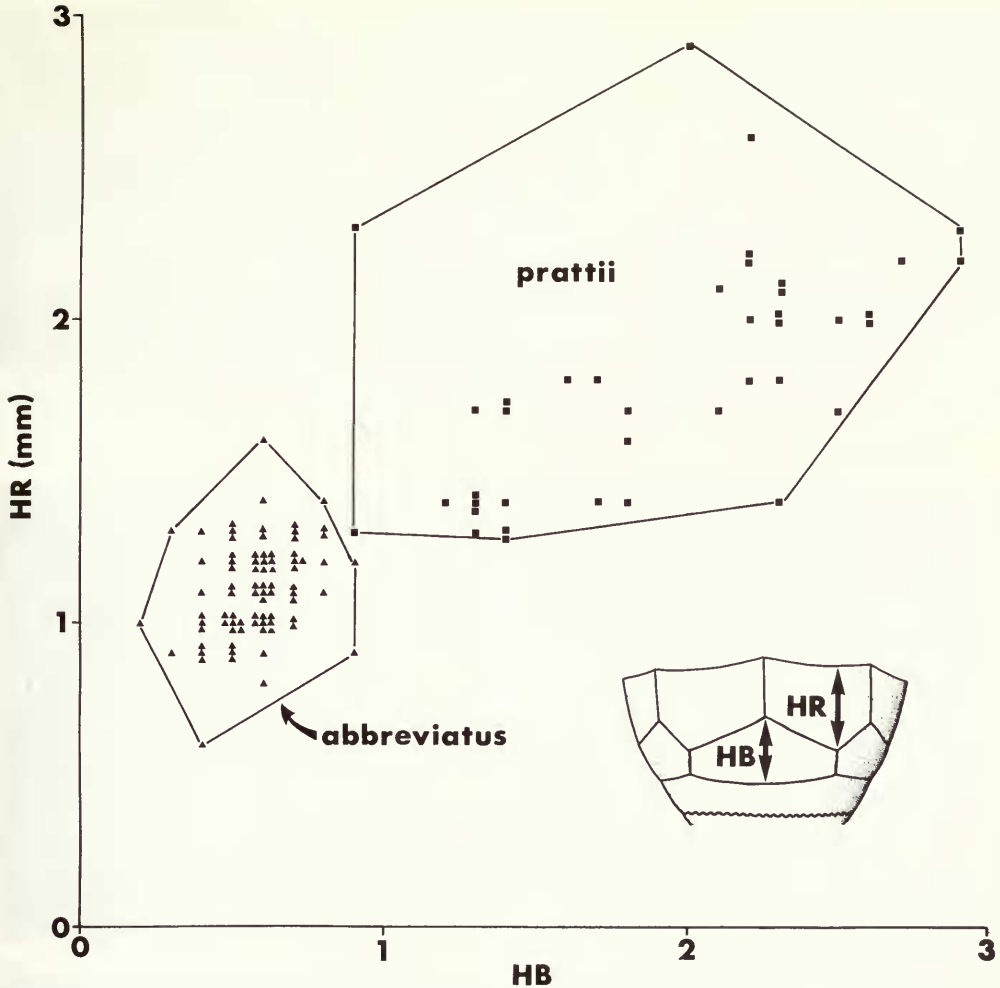
Fig. 16 Height of basals plotted against height of radials in *Ailsacrinus abbreviatus* gen. et sp. nov. and *A. prattii* (Gray).

but has radiating rows of tubercles (Fig. 19). The proximal facet of the top columnal, articulating with the basals, is a weakly marked symplexy or cryptosymplexy in *A. abbreviatus* but more strongly marked in *A. prattii*. The high pyramidal form of this facet suggests permanent attachment of the columnal to the cup, i.e. that the topmost columnal is a proximale. However, the columnal is not united to the cup by a synostosis as in the Recent crinoids discussed by Breimer *in* Ubaghs *et al*. (1978: T25).

Dorsal cup

The cup is small and bowl-shaped (Ubaghs *in* Ubaghs *et al*. 1978: fig. 72) in *A. abbreviatus* (Fig. 46, p. 66), rather larger and more conical in *A. prattii* (Fig. 5). A depressed base (Fig. 15) accommodates the pyramidal facet of the top columnal. Syntaxial overgrowths obscure details of the adoral interior of the cup in all specimens examined. However, external preservation of plates is good.

Basals are very small and triangular in *A. abbreviatus*. Externally, adjacent basals either fail to touch or barely touch one another (Figs 12–14). They are seen, however, to make contact internally in specimens whose stems have been removed (Fig. 15). Basals of *A. prattii*, though
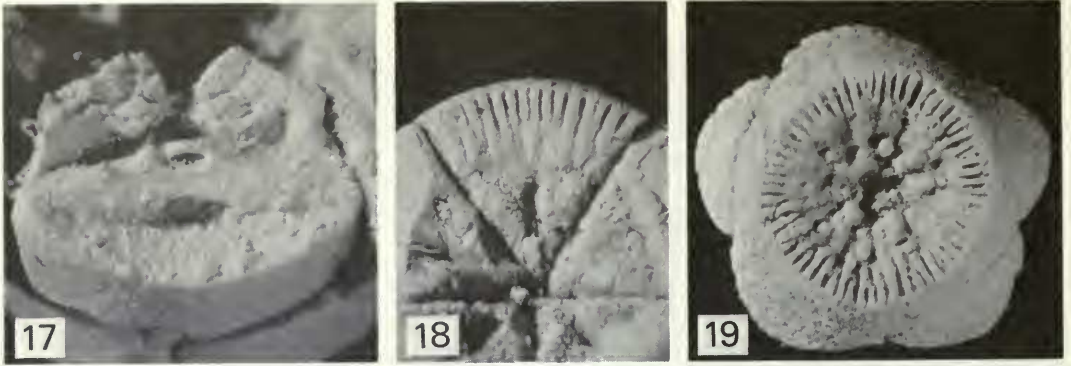
Figs 17–19 *Ailsacrinus prattii* (Gray), Great Oolite, Lansdown Hill. Specimens coated with ammonium chloride. Fig. 17, SM J33707, radial facet; ×11. Fig. 18, SM J33703, basal facet; ×8. Fig. 19, SM J33708, distal facet of top columnal; ×7.
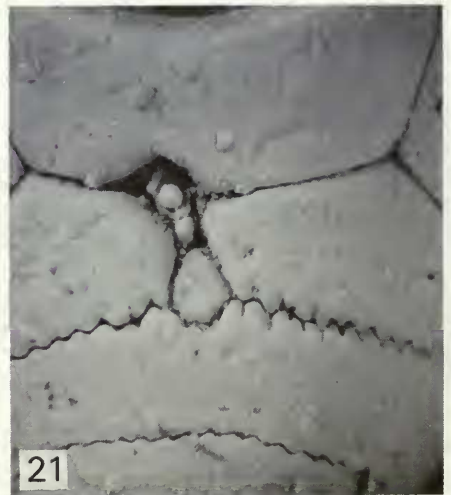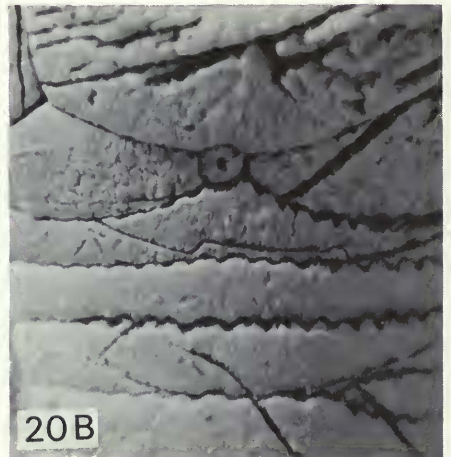
Figs 20–21 *Ailsacrinus pratti* (Gray), Great Oolite, Lansdown Hill. Specimens coated with ammonium chloride. Fig. 20, SM J33695: A, long stem with 5 lenticular columnals (arrowed); ×3·9; B, proximal columnals and tuberculate accessory plate; ×12. Fig. 21, SM J33700, ray containing several irregular accessory plates, one of which is tuberculate; ×12.

also reduced in size, are larger and touch adjacent basals externally giving them a five-sided external shape (Figs 5–8). The proximal facet of each basal has a median radial depression and a marginal crenularium which, like the facet of the adjoining columnal, is well-developed in *A. prattii* (Fig. 18) but poorly-developed in *A. abbreviatus* (Fig. 15). The facet between basals and radials has not been observed.

Radials exceed the height of basals in *A. abbreviatus* but are of about the same height in *A. prattii* (Fig. 16). Their distal articulating facet (i.e. that which articulates with the first brachials) is inclined at a variable angle to the long axis (proximal–distal) of the crinoid. An angle of 15° has been estimated in *A. abbreviatus* and angles between 30° and 60° in *A. prattii*. This variability may relate, at least in part, to the attitude of burial and the nature of plate disarticulation during compaction. Radial facets have a deep aboral ligamental fossa, small interarticular ligamental fossae and large muscular fossae (Fig. 17).

In addition to the usual plates of the cup, small accessory plates are a characteristic feature of *Ailsacrinus*. These seem to be present in a minority of individuals of *A. abbreviatus* where they are generally inconspicuous, but are present in most specimens of *A. prattii*. Those individuals of *A. abbreviatus* with accessory plates do not usually have them in every ray. Accessory plates are more numerous in *A. prattii*, some individuals having up to 3 or 4 plates per ray (Fig. 21). Their position is perradial, i.e. between basals. Sometimes the accessory plates are in contact with the top stem columnal (Figs 20B, 22), particularly in *A. abbreviatus* where the basals are small and not contiguous. In *A. prattii* accessory plates are often located at a triple junction between two basals and a radial (e.g. right-hand accessory plate of Carpenter 1882: pl. 1, fig. 3), or they may be extended distally into embayments within radials (Fig. 21). Large accessory plates in some *A. prattii* specimens are located in the basal circlet in contact with both column and radials (e.g. left-hand accessory plate of Carpenter 1882: pl. 1, fig. 3). Several specimens of *A. prattii* have shallow pits in the cup which are in appropriate locations to have accommodated large accessory plates (Fig. 5). Most are vacant but some are occupied by small accessory plates. An interesting feature of the accessory plates is the presence of tubercles on some of them. These resemble the spine-bearing tubercles of echinoids in having a mamelon and a central foramen (Fig. 12C). The sporadic occurrence of accessory plates led Carpenter (1882: 35) to suppose that they were 'without any morphological importance'. However, they seem to be present in too many individuals for Carpenter's opinion to be acceptable. Among living crinoids they would appear to have no close analogues. Andrew Smith (personal communication 1981) has suggested a comparison with statocysts, balancing structures developed in several groups of echinoderms. Kirk (1911) identified accessory plates as infrabasals. Some specimens of *A.*

Figs 22–24 *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Specimens coated with ammonium chloride. Fig. 22, BMNH E68076, unusually large accessory plate and poorly-preserved radial facet; × 17. Fig. 23, BMNH E68077, facet of the most proximal syzygy (on the distal side of secundibrach 4) showing numerous culminae; × 18. Fig. 24, BMNH E68078, oral pinnules lying across the adoral surface of the calyx; × 12.

4*

abbreviatus have tabular plates concealed between the basals which resemble the infrabasals of *Liliocrinus polydactylus* (d'Orbigny) illustrated by Ubaghs *in* Ubaghs *et al.* (1978: fig. 73,5). However, their relationship with accessory plates is unclear.

Tegmen

Definite tegminal plates have not been identified in *Ailsacrinus*, although a mass of small plates originally above the displaced calyx in a specimen of *A. prattii* (SM J33712) may include tegminal plates as well as pinnulars. Alternatively, the tegmen in *Ailsacrinus* may have been like that of many living comatulids, i.e. naked with the exception of microscopic skeletal elements.

Arms

Arm morphology was discussed little by Carpenter (1882), whose material consisted mostly of Lansdown crinoids lacking arms or with disarticulated brachials. In contrast, the specimens of *A. abbreviatus* from Northleach often display finely-preserved arms (Figs 25–27). In several
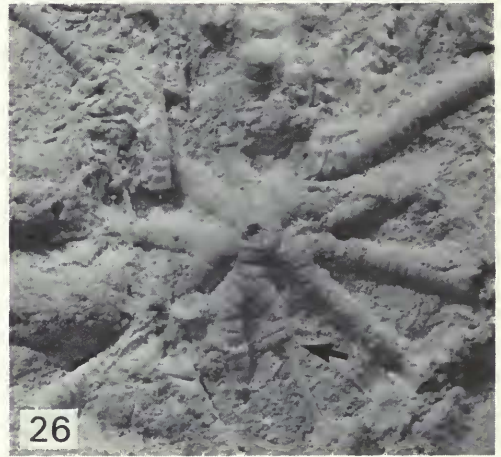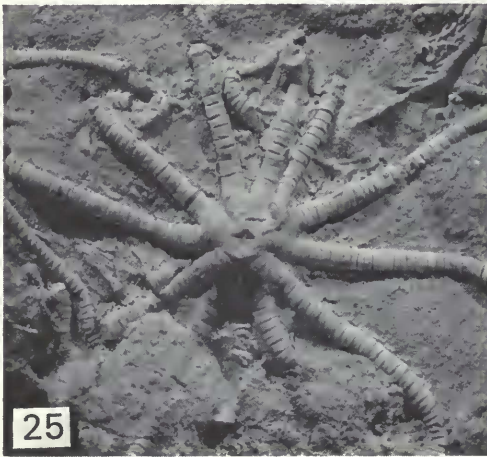
Figs 25–27 *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 25, **Holotype** BMNH E67797, cup and radially-arranged arms (eleven-armed appearance is due to the presence of an arm from a second individual); ×1. Fig. 26, BMNH E67808, crinoid with regenerated arm arising from the most proximal syzygy (arrowed); ×1·6. Fig. 27, BMNH E67794, pinnulated arm resting on a bedding plane; ×2·1.
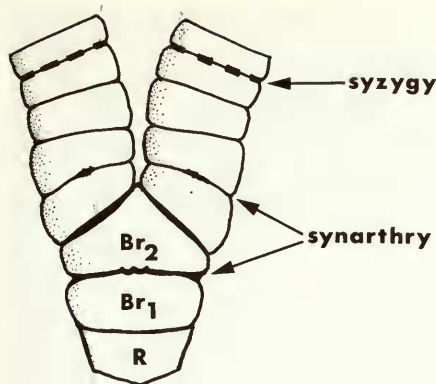
Fig. 28 Diagram showing proximal brachial articulations in *Ailsacrinus* gen. nov. With the exception of the synarthries and the syzygy all articulations are muscular. R, radial; Br_1, 1st primibrach; Br_2, 2nd primibrach.

individuals these seem to be almost completely preserved, interrupted only by minor disarticulation and dislocation. However, the tendency for arms to be preserved lying oblique to bedding means that their entire length is never seen. There would appear to be no significant difference in arm structure between *A. abbreviatus* and *A. prattii*. Both have identical patterns of articulation and similarly-shaped brachials, though rather larger in *A. prattii*. The arms divide only once and hence *Ailsacrinus* is ten-armed. Arms in *A. abbreviatus* have been observed to exceed 19 cm in length.

The first primibrach has a muscular articulation with the radial, and the second primibrach is an axillary (Fig. 28). Therefore the first brachitaxis contains two brachials, a common condition in articulate crinoids. However, an *A. prattii* specimen (SM J33709) illustrated by Carpenter (1882: pl. 1, fig. 23) has two rays containing a third primibrach. A single ray of an *A. abbreviatus* individual (BMNH E68072) contains only one primibrach, the axillary, in the first brachitaxis. These rare variants may be meristic or perhaps pathological.

Articulations between primibrachs 1 and 2, and between secundibrachs 1 and 2, are synarthrial (Fig. 28). Synarthrial facets have depressed ligamental fossae on either side of a fulcral ridge with an adoral–aboral orientation (Fig. 30). Stereom of the ligamental fossae does not show well-defined galleries in specimens examined by electron microscope (Fig. 31).

A second kind of nonmuscular articulation occurring commonly in the arms of *Ailsacrinus* is a syzygy. The first syzygy (Fig. 28) is situated between secundibrachs 4 and 5 (unlike in comatulids, where it generally occurs between secundibrachs 3 and 4; Rasmussen *in* Ubaghs *et al.* 1978) and subsequent syzygies are present at frequent intervals along the arm. On average, about 25% of joints are syzygial, and the intersyzygial interval is 2, 3 or 4 muscular joints. Some, but not all, lengths of arm of *A. abbreviatus* display a regular pattern (Fig. 32) of syzygies separated alternately by 2 and 4 muscular joints.

Syzygial facets have a series of culmina radiating from the axial canal (Figs 23, 33, 34A, B). The number of culmina per facet is variable, ranging from about 7 (Fig. 34A) to 20 (Fig. 23). Occasionally, the culmina are reduced to a row of tubercles, in the manner of isocrinid cryptosyzygies (Breimer *in* Ubaghs *et al.* 1978: T38). Culmina of adjoining brachials are clearly seen to oppose (Figs 35A, B). Stereom of the culmina is dense and consists of closely-spaced broad rods, 15–20 μm in width, linked by small cross-struts (Fig. 34C); orientation of the rods is approximately concentric about the axial lumen. This results in some of the rods being oblique to the culmina on which they are situated. Culmina stereom appears to have been strong and capable of resisting abrasion caused by adjacent brachials rubbing against one another. Though similarly dense, stereom of the culmina in the living comatulid *Nemaster rubiginosa* (Macurda, Meyer & Roux *in* Ubaghs *et al.* 1978: fig. 191,4) contrasts with that of *Ailsacrinus* in having a knobbly appearance without a directional fabric. Stereom of the crenellae, which is presumed to have served as an anchorage for ligament, in *Ailsacrinus* appears to be galleried with a pore diameter of about 5 μm (Fig. 34C).
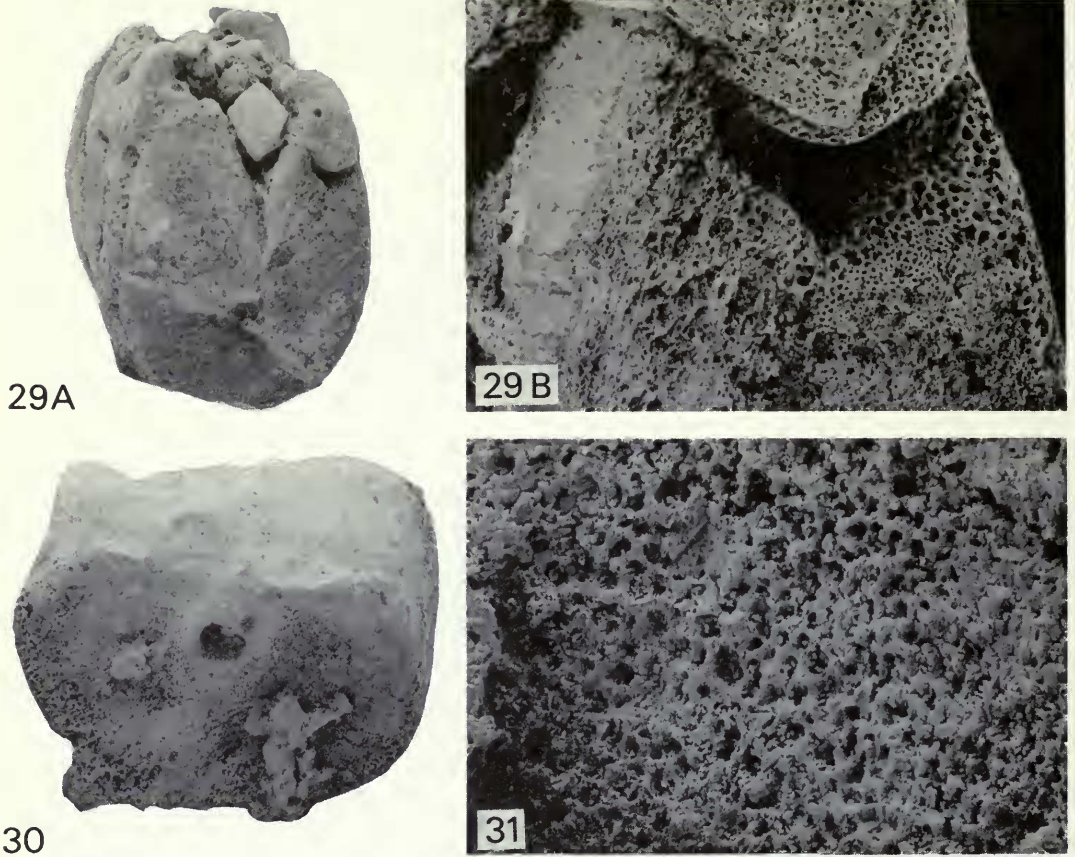
Figs 29–31 Scanning electron micrographs of muscular and synarthrial articulations in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 29, BMNH E68079: A, poorly-preserved, moderately oblique muscular facet; ×10·8; B, fine stereom of the muscular fossa; ×67. Figs 30–31, BMNH E68074: Fig. 30, synarthrial facet; ×25; Fig. 31, stereom of the ligamentary fossa of a second synarthrial facet; ×185.
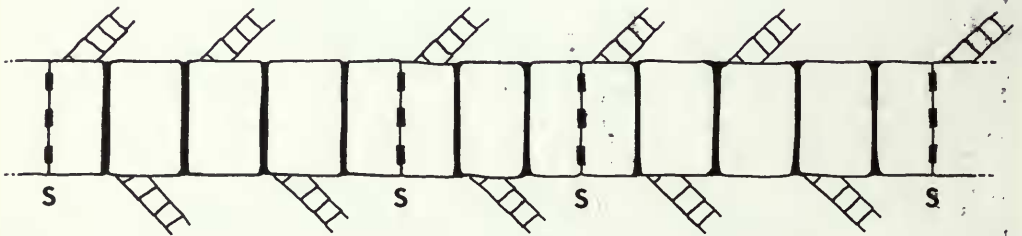

Fig. 32 Diagram showing a common pattern of distribution of brachial articulations and pinnules in the arms (viewed aborally) of *Ailsacrinus abbreviatus* gen. et sp. nov. Syzygies are beaded and labelled 'S'; the remaining articulations are muscular.

Brachials situated proximally and distally of a syzygy, hypozygals and epizygals respectively, are rather narrower than other brachials (Fig. 35A). When arm regeneration is observed, the regenerated arm always arises from a syzygial joint, in one instance from the most proximal syzygy in the arm (Fig. 26). Regeneration from a syzygy was illustrated by Jelly (1833: figs 4, 5) and is a characteristic of most living crinoids (Breimer *in* Ubaghs *et al.* 1978: T34).
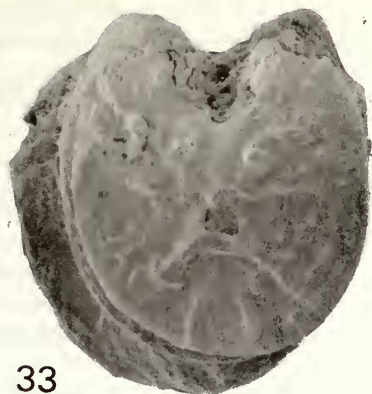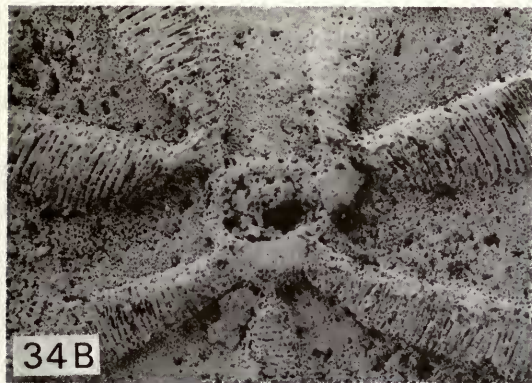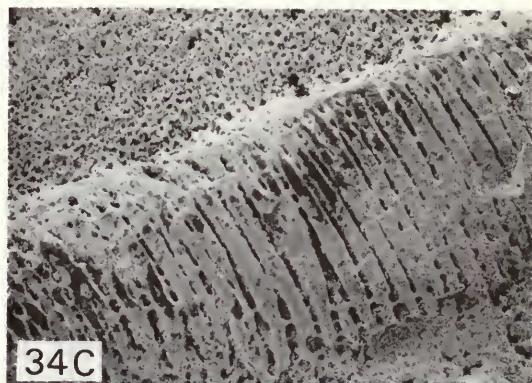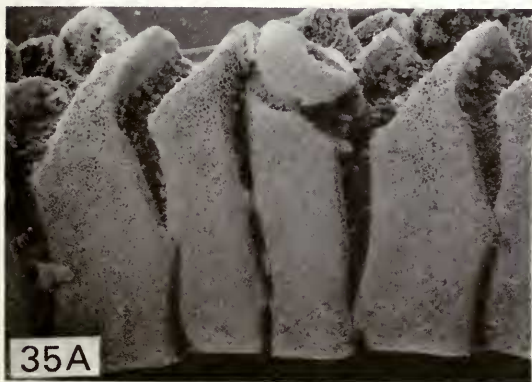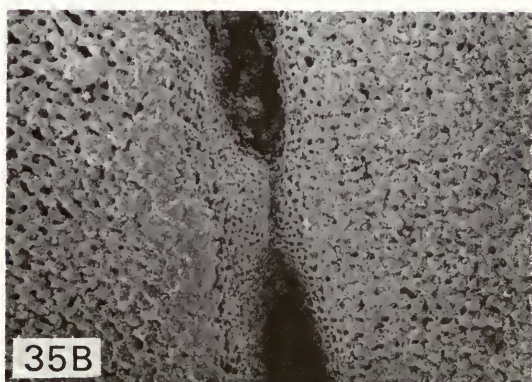
Figs 33–35 Scanning electron micrographs of syzygial articulations in *Ailsacrinus* gen. nov. Fig. 33, *A. prattii* (Gray), BMNH E5722 (fragment), Great Oolite, Lansdown Hill; syzygial facet with poorly-developed culminae; ×15. Fig. 34, *A. abbreviatus* sp. nov., BMNH E68080, Bathonian (? Sharps Hill Fm.), Eastington: A, syzygial facet with well-developed culminae; ×18·5; B, culminae radiating from the axial canal; ×52; C, stereom of culmina and crenellae; ×130. Fig. 35, *A. abbreviatus* sp. nov., BMNH E68081, Bathonian (? Sharps Hill Fm.), Eastington: A, lateral view of an arm showing narrow hypozygal and epizygal brachials; ×10·4; B, opposing culminae of hypozygal and epizygal; ×56.

Muscular facets are rarely observed in *A. abbreviatus* because pre-fossilization arm breakage invariably occurred at syzygies and articulated brachials are now firmly bound together with syntaxial calcite overgrowths. Unfortunately stereom preservation is poor in Lansdown *A. prattii* where muscular articulation facets are more commonly visible. Muscular articulations in

Ailsacrinus are slightly to moderately oblique. Facets show a large aboral ligamental fossa and have an adoral region above the fulcral ridge where a poorly-defined break in slope appears to separate large interarticular ligamental fossae from small muscular fossae (Fig. 29A). A layer of fine stereom apparently overlies coarser stereom in the muscular fossa of a poorly-preserved specimen of *A. abbreviatus* (Fig. 29B).

Pinnules

Pinnulation in *Ailsacrinus* is relatively complete. The two primibrachs and secundibrach 1 lack pinnules, and so the first pinnule arises from secundibrach 2. Thereafter pinnules arise on alternate sides of the arm from each brachial, with the exception of hypozygals preceding syzygies. The distribution of syzygies means that along each side of the arm, pinnules are borne on either every second or on every third brachial (Fig. 32). There are at least two distinct types of pinnules in *Ailsacrinus*, an oral series and a distal series.

Oral pinnules occur in the proximal parts of the arms and are generally found lying across the adoral surface of the calyx (Fig. 24). There seem to be two or three pairs of oral pinnules on each arm. Although complete oral pinnules have not been seen, their preserved length and taper suggests that they are shorter than distal pinnules. Oral pinnules lack ambulacral grooves and associated cover plates, and their pinnulars are short and high. Each pinnular has an adoral
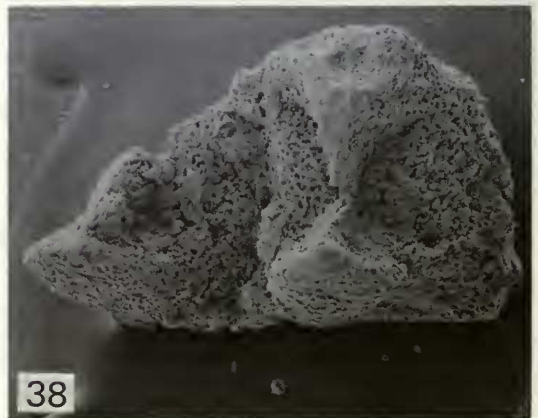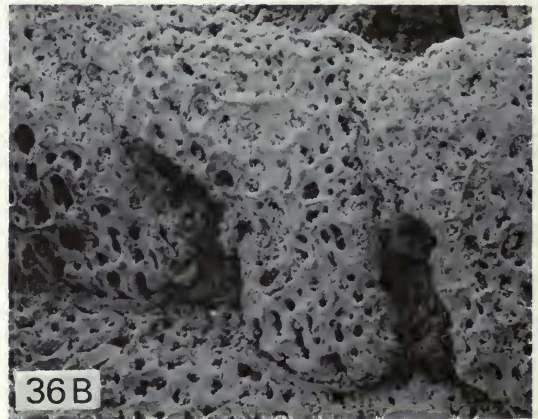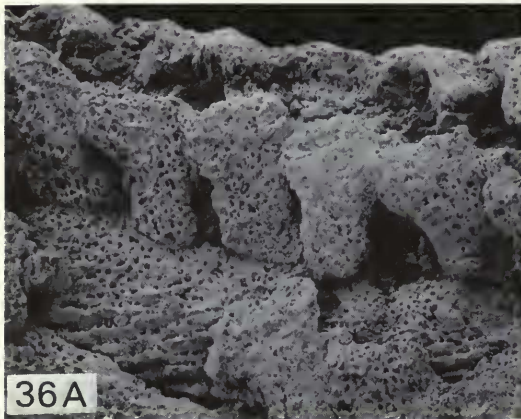
Figs 36–38 Scanning electron micrographs of pinnulars and cover plates in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 36, BMNH E68082; A, boot-shaped cover plates; × 75; B, coarse, irregular cover plate stereom; × 180. Fig. 37, BMNH E68083, rectangular cover plates collapsing into the ambulacral groove; × 62. Fig. 38, BMNH E68084, fragment of an oral pinnule with one complete pinnular and part of a second pinnular; × 53.

median transverse ridge (Fig. 38), broad at the two outer edges of the pinnular and narrow at the centre. Coarse stereom flanks the ridge. In profile, this ridge forms a triangular-shaped top to the pinnular. The nature of articulations between oral pinnulars is unknown. The function of oral pinnules in living crinoids is unclear but they may have roles in defence, manipulation of food particles, and/or fixation.

Distal pinnules have ambulacral grooves and are composed of comparatively elongate pinnulars (Fig. 39A). The maximum observed length of a distal pinnule in *A. abbreviatus* is over 2 cm in an incomplete pinnule composed of 28 pinnulars. However, another distal pinnule in the same species was complete and consisted of 21 pinnulars. Distal pinnules are terminated by a pinnular which tapers to a point. The articulation between brachials and pinnular 1 is muscular with a fulcral ridge orientated almost parallel to the length of the arm. The articulation between pinnulars 1 and 2 is also muscular but the articulation between pinnulars 2 and 3 is synarthrial. The presence of a large aboral ligament is responsible for the gap commonly observed between the short pinnular 1 and pinnular 2, when viewed from the side (Fig. 39B). Stereom on the outer sides of distal pinnulars is fascicular (Fig. 39C), rather like that of syzygial culmina but contrasting with stereom of the brachials (Fig. 39D). Broad rods (15–20 μm in width) connected by cross-struts parallel the length of the pinnular and are orientated slightly obliquely to the surface of the pinnular. The rods have distally directed pointed ends (Fig. 39C). Minute rectangular or boot-shaped cover plates border the ambulacral groove (Figs 36A, B, 37).
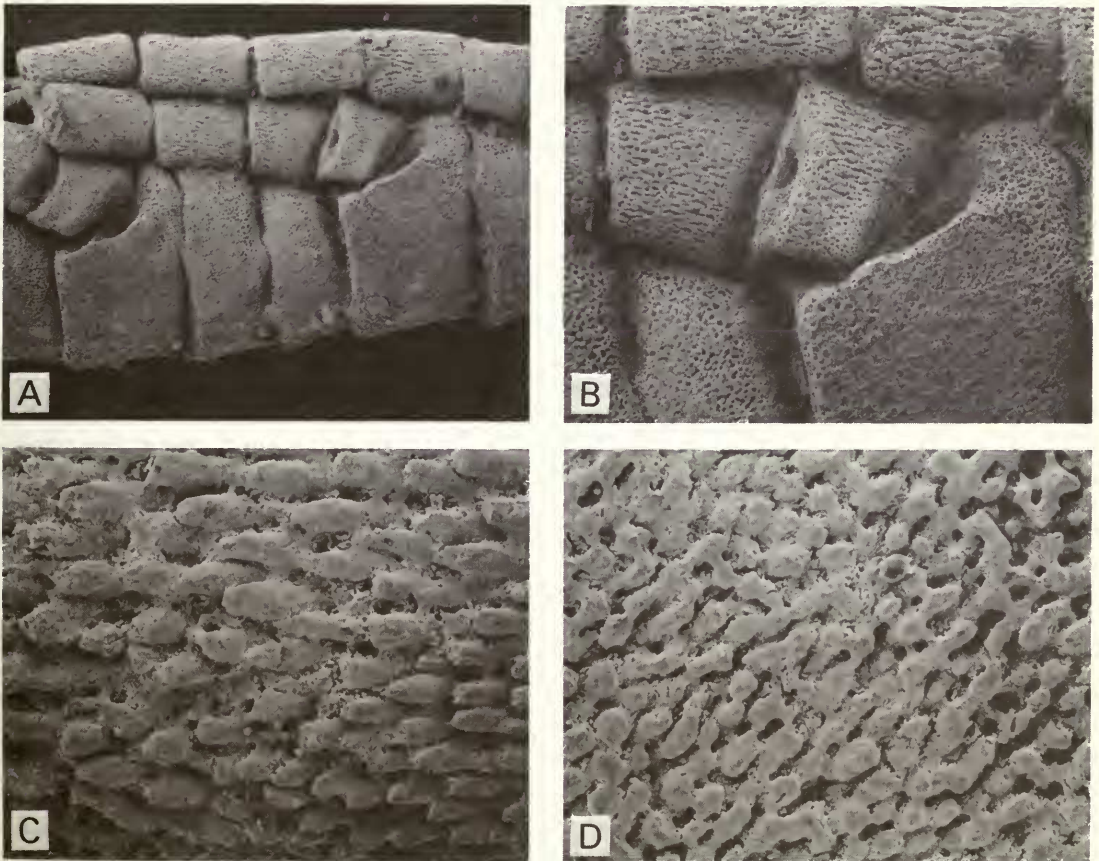

Fig. 39 Scanning electron micrographs of brachials and distal pinnules in *Ailsacrinus abbreviatus* gen. et sp. nov., BMNH E68083, Bathonian (? Sharps Hill Fm.), Eastington. A, general view; × 16·4. B, prominent aboral ligament fossa visible between first and second pinnulars; × 34. C, fascicular stereom of pinnular; × 175. D, brachial stereom; × 175.

Depending on their length, each pinnular may have two, three or even four pairs of cover plates. The stereom of cover plates is irregular and labyrinthic, with a pore diameter between 3 and 20 μm (Fig. 36B).

In some specimens of *A. abbreviatus*, pinnules situated immediately distal to the oral pinnules do not usually have preserved cover plates although they are otherwise indistinguishable from typical distal pinnules. By analogy with living comatulids (Breimer *in* Ubaghs *et al.* 1978: T43), the position of these pinnules suggest that they may have been genital pinnules.

Reconstruction

The appearance of a complete *A. abbreviatus* individual is reconstructed in Fig. 40. Of particular note is the disproportionately short stem relative to arm length.

Colour

Individuals of both *A. prattii* from Lansdown and *A. abbreviatus* from Northleach may be conspicuously coloured. Their colour varies from pale grey-purple to dusky red-purple and is usually restricted to the calyx and column. One side of the crinoid is sometimes more deeply coloured than the other (e.g. BMNH E5722) and distribution of the colour may be patchy. It seems possible that this colouration is a remnant of an original pigmentation. Living crinoids are often deeply pigmented (Hyman 1955) and, although pigmentation is fugitive (spirit-preserved specimens tend to lose their colour), it is known that organic pigments can survive fossilization in crinoids. Blumer (1960, 1962) extracted hydrocarbon pigments, 'fringelites', from U. Jurassic *Millericrinus*. He interpreted their preservation as indicating a strongly reducing environment beneath the sediment–water interface. Proof that the colouration of *Ailsacrinus* is due to similar organic pigments would necessitate time-consuming chemical analysis which has not been undertaken. However, it may be significant that the largest specimen of *A. abbreviatus* (BMNH E67807) from Northleach is also the most intensely coloured; living crinoids concentrate pigment during life and thus become more deeply coloured as they grow.

Stem ontogeny

Undoubtedly the feature of *Ailsacrinus* that has attracted most attention is the highly variable stem. Hypotheses regarding the ecology of *Ailsacrinus* must take into account stem morphology and variability. Stem morphology observable in specimens of *Ailsacrinus* is the outcome of ontogenetic processes which acted during the life of the crinoids.

It is thought that all crinoids pass through a stage during their development when they are fixed firmly to the substrate by means of a stem or column. In the cystidean and pentacrinoid stages of early ontogeny in comatulids (Breimer *in* Ubaghs *et al.* 1978), the column may possess many and well-differentiated columnals. For example, John (1938) describes a pentacrinoid of the comatulid *Notocrinus virilis* Mortensen with a crown 2·2 mm long and a 10 mm long column comprised of 45 columnals. Comatulids end their pentacrinoid stage when autotomy causes the crown to break free of the column. However, in stalked crinoids the crown remains attached to the column and a pentacrinoid stage may not be readily distinguishable (Breimer *in* Ubaghs *et al.* 1978: T56).

The early ontogeny of *Ailsacrinus* was most probably like that of comatulids, with a fixed pentacrinoid stage followed by a free-living adult stage. The duration of the fixed stage may have been short, as in comatulids, or more protracted. Kirk (1911: 49) believed that detachment took place in late ontogeny, not much earlier than crinoids represented in some of Carpenter's (1882) figures of small *Ailsacrinus* individuals. If the supposed 'root' of *A. prattii* (Carpenter 1882: pl. 1, fig. 5) is truly a holdfast, then Kirk's belief may be correct because the structure possesses apparent columnals of a moderately large size. However, in the absence of small individuals there is no way of confirming or refuting this suspicion.

Stem growth in stalked crinoids is achieved by the formation of new columnals together with accretionary growth of existing columnals (Ubaghs *in* Ubaghs *et al.* 1978: T82). *Ailsacrinus* has a homomorphic stem (nodals and internodals are not recognizable), apparently with a fused top
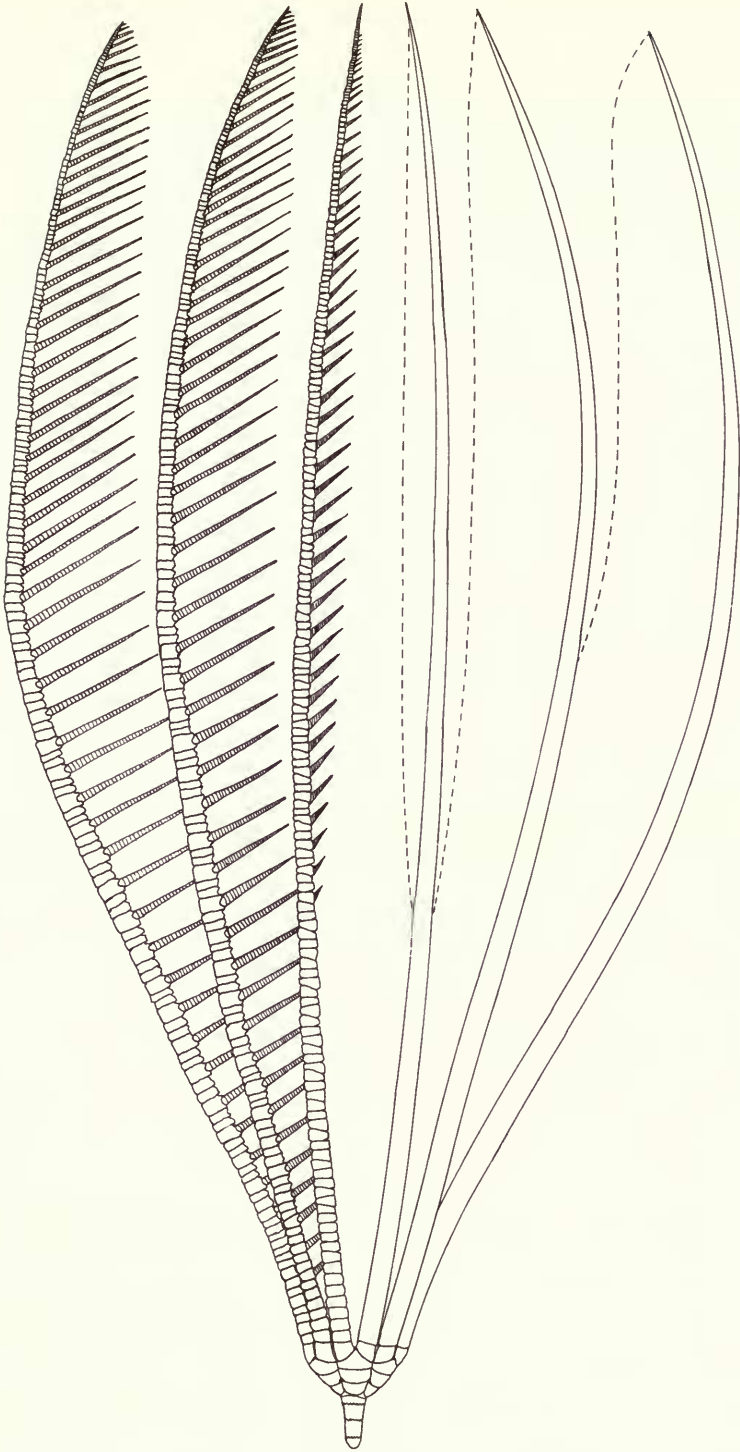
Fig. 40   Reconstruction of *Ailsacrinus abbreviatus* gen. et sp. nov. Arms have a total length of about 15–20 cm and are depicted in an arbitrary orientation which was not necessarily their position during feeding.

columnal or proximale. In this type of stem, columnal addition is localized to a generating area immediately beneath the proximale. Continued columnal addition pushes earlier columnals further down the stem and gives a proximal–distal gradient of increasing columnal age. The initial width of each new columnal is equivalent to that of the proximale at the time of columnal formation, i.e. about the same width as the base of the cup. Enlargement of the generating area during ontogeny causes new columnals to become successively wider. If this were the only factor controlling columnal width the stem would taper away from the cup. However, a second factor is the accretionary growth of existing columnals. This factor in isolation would produce a stem which tapered towards the cup because older columnals are situated furthest from the cup. Final stem-form is a result of interaction between these two factors (see Seilacher, Drozdzewski & Haude 1968). Axial growth in columnal height occurs concurrently with transverse columnal growth. If all new columnals initially had the same height, then there should be a proximal–distal gradient of increasing columnal height towards older columnals situated near the base of the stem.

Reduction in length of the stem is a further possibility in crinoids especially pertinent in the case of *Ailsacrinus*. This could result from either the shedding of whole columnals (cf. isocrinids; Rasmussen 1977) by autotomy or accident, or columnal resorption. Bather (1900: 191) said of *A. prattii* 'the crown breaks off from the root, the stem is gradually resorbed, and a free-floating stage attained'. Kirk (1911: 49) believed that the column was shortened by 'the dropping off of some of the distal columnals accompanied by more or less resorption'.

Consequently, there are three main possibilities for post-detachment stem ontogeny in *Ailsacrinus*:

1. stem lengthening by addition of columnals, and/or growth of existing columnals,
2. no change in stem length, or
3. stem shortening by shedding columnals and/or resorption.

Several lines of enquiry can be followed to decide which of these is the most likely.

Evidence from single crinoids

LENTICULAR COLUMNALS. Some individuals of both species have stems with incomplete or lenticular (Carpenter 1882) columnals. These columnals, instead of extending all the way around the circumference of the stem, when traced laterally in either direction are seen to 'pinch-out' or boudinage. They may be of slight lateral extent (Fig. 10) or may encompass most of the stem (Fig. 20A). A specimen of *A. prattii* (Fig. 20A), incorrectly drawn by Carpenter (1882: pl. 1, fig. 7), has four lenticular columnals aligned exactly above one another and alternating with complete columnals. Lenticular columnals are not exclusive to *Ailsacrinus*; de Loriol (1877–9) figured similar structures in *Millericrinus* and *Apiocrinus*.

Carpenter (1882: 33) regarded lenticular columnals as columnals in the process of formation, i.e. columnals fossilized in an early ontogenetic state. If this opinion is correct then the occurrence of lenticular columnals points to columnal addition during late ontogeny, probably after detachment.

Little is known of the process of columnal addition in crinoids. Ubaghs (*in* Ubaghs *et al.* 1978: fig. 60, 1, 2) illustrates longitudinal sections through juvenile and mature portions of the column of Silurian *Barrandeocrinus*. In the juvenile column, new columnals are present as thin discs which taper away from the column axis and are not visible at the surface. The mature column has columnals of even thickness, all reaching the surface of the column. Columnals are apparently introduced in a similar manner in articulates (Rasmussen *in* Ubaghs *et al*. 1978: T269), beginning as thin concealed discs. These immature columnals are clearly unlike the lenticular columnals of *Ailsacrinus*. Growth of lenticular columnals to completion and uniform thickness would necessitate transfer of skeletal material from adjacent thickened columnals (Fig. 41). This complication suggests that lenticular columnals are not columnals in the process of formation. Further evidence against Carpenter's hypothesis comes from the distribution of lenticular columnals which are often found distal to the expected site of columnal addition
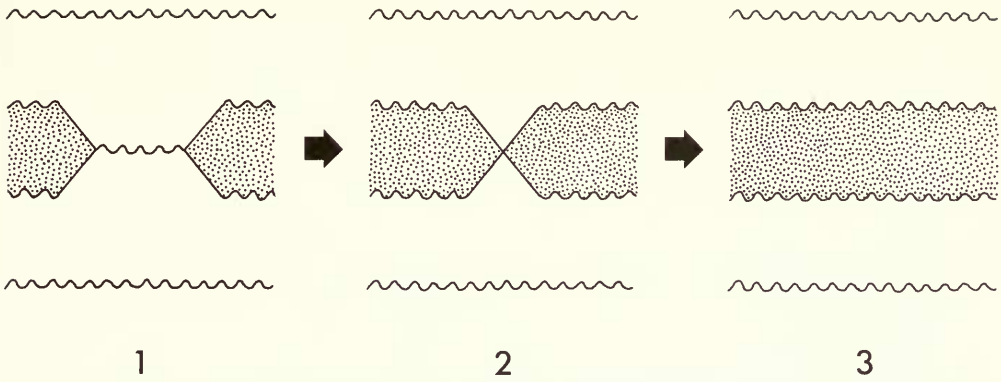
Fig. 41 Three-stage diagram showing that growth to completion of lenticular columnals of the type depicted in Fig. 20A (p. 50) would occur at the expense of adjoining columnals.

immediately beneath the proximale. Therefore, no significance can be given to lenticular columnals in stem ontogeny.

Variation in columnal size. Gradients of change in columnal size in a proximal–distal (young–old) direction are readily quantifiable in long-stemmed individuals of *A. prattii*. Turning first to columnal height, the usual pattern is one of decreasing height in a distal direction away from the cup (J33695 of Fig. 42), i.e. presumed older columnals are shorter than younger columnals. However, in at least one specimen (SM number J33694 of Fig. 42) columnal height increases away from the cup, i.e. presumed older columnals are taller than younger columnals. The occurrence of this reverse trend means that columnal height cannot be used as a reliable indicator of columnal age and provides no useful information about stem ontogeny pre- or post-detachment.
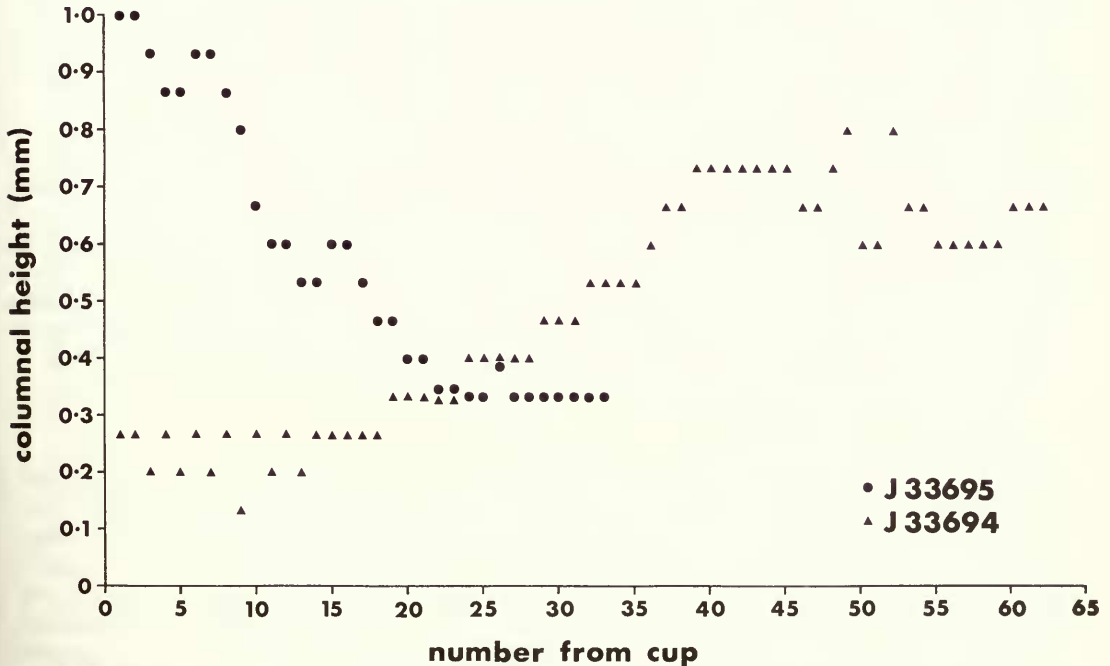
Fig. 42 Change in columnal height away from the cup in two long-stemmed individuals (SM J33695 and J33697) of *Ailsacrinus prattii* (Gray).
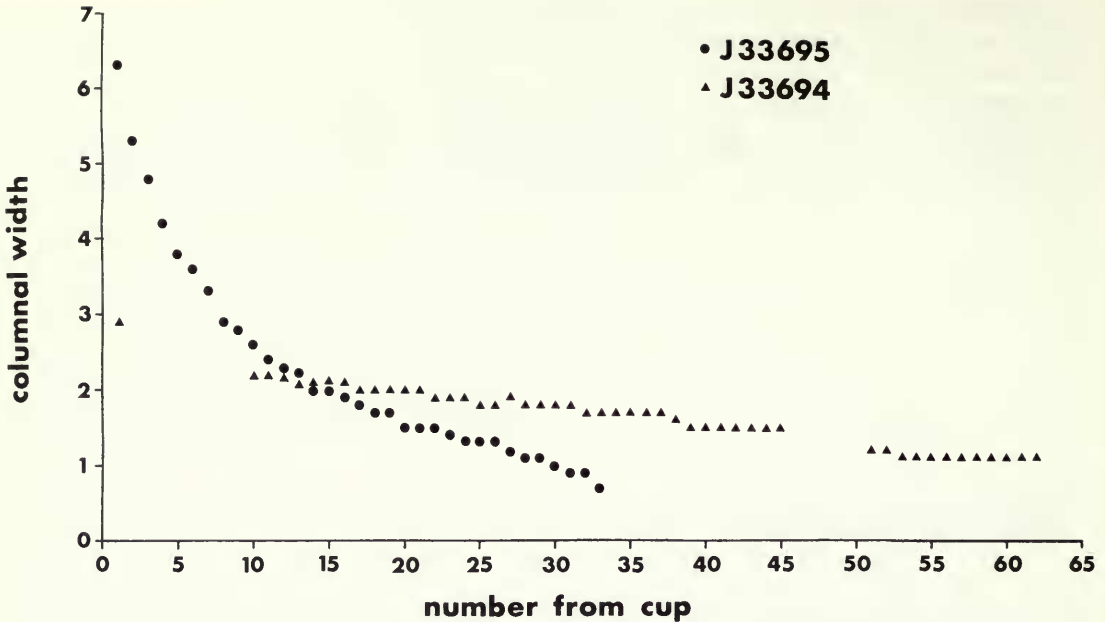
Fig. 43   Change in columnal width away from the cup in two long-stemmed individuals (SM J33695 and J33697) of *Ailsacrinus prattii* (Gray).

Columnal width always decreases away from the cup (Fig. 43), as is shown by the distal taper of *Ailsacrinus* stems. Stems with fewer columnals are generally found to taper more steeply than stems with a large number of columnals (cf. Figs 7 and 20A). If the width of columnals were proportional to the size of the generating area, then this proximal–distal size gradient would reflect addition of successively wider columnals as the crinoid grew. However, the second factor of accretionary growth after inception must be taken into account. Even if no new columnals were added after detachment, some amount of accretionary growth is likely to have occurred in order that stem width should keep pace with increasing cup width. Consequently, columnal width gradients do not help in resolving the problem of stem ontogeny.

DISTALMOST COLUMNAL. The columnal terminating the stem in *Ailsacrinus* most typically has a blunt, rounded end (Figs 8, 11). In some short-stemmed individuals of *A. abbreviatus*, however, the distalmost columnal has a worn quinquelobate symplectial facet (Fig. 13) which may have been a life condition rather than a result of preburial stem fracturing. The axial lumen may be exposed or occluded at the base of this columnal. It has not been possible to identify dense fabrics indicative of resorption but this may be due to poor preservation of stem stereom. However, it is clear from the general shape of the distalmost columnal that it has undergone some sort of modification, though this could be the result of any combination of post-detachment columnal growth, resorption and mechanical abrasion.

Evidence from crinoid populations

Assuming size to be a reasonable indicator of the age of a crinoid, comparisons of stem length between individuals of differing size should throw light on post-detachment ontogeny of the stem in *Ailsacrinus*. The overall size of the crinoid is impossible to determine even in these exceptionally well-preserved crinoids. A frequently employed measure of crinoid size, that of the dimensions of the dorsal cup (e.g. Roux 1978), is not suitable in *Ailsacrinus* because it is influenced by burial attitude – the cup is shortened and splayed outwards in crinoids buried upright relative to crinoids buried prostrate. In order to quantify crinoid size the dimension chosen was the height of the axillary brachial, an easily defined and measured parameter which would appear to have no causal correlative link with stem length.
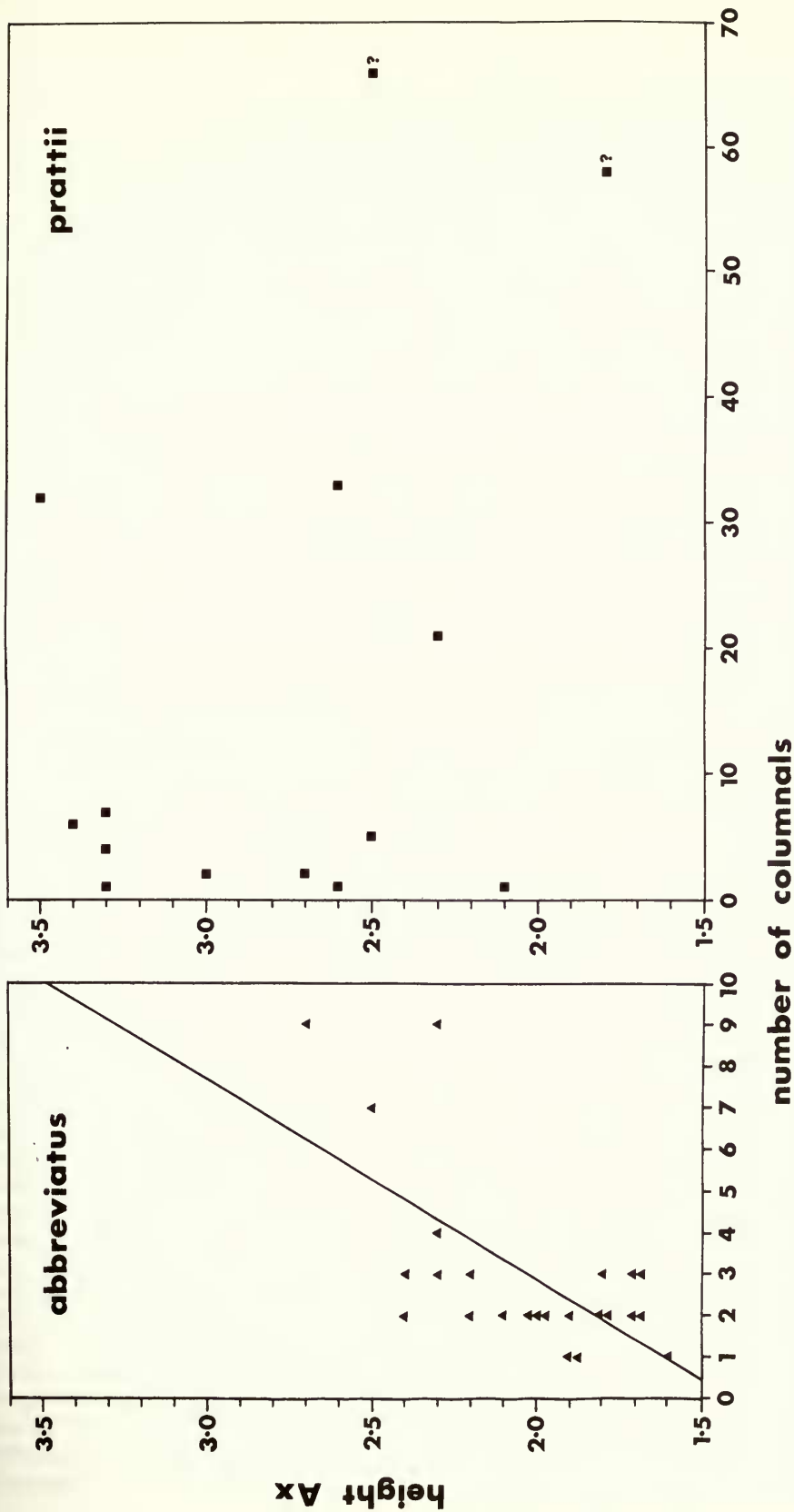
Fig. 44 Plots of crinoid size (expressed as height of the axillary brachial) against stem length (expressed as number of columnals) in 24 specimens of *Ailsacrinus abbreviatus* gen. et sp. nov. from Eastington and 14 specimens of *A. prattii* (Gray) from Lansdown Hill. Stem length is positively correlated (R = 0·652) with crinoid size in *A. abbreviatus* and the reduced major axis regression line has been fitted to the data points. There is no significant correlation (R = 0·395) between stem length and crinoid size in *A. prattii*.

Number of columnals and height of the axillary brachial were determined in 24 specimens of *A. abbreviatus* from Eastington and 14 specimens of *A. prattii* from Lansdown. These parameters were found to be positively correlated in the *A. abbreviatus* sample but not so in the *A. prattii* sample where there is a wide scatter of points (Fig. 44). Therefore, the *A. abbreviatus* data are consistent with an ontogenetic net increase in columnal number (i.e. columnal addition exceeding columnal shedding) but a similar hypothesis is not supported by data from the longer-stemmed *A. prattii*. But this result is suspect because of the probable existence of high levels of non-ontogenetic variation (e.g. in accessory plate and lenticular columnal development) within populations of *Ailsacrinus*. This non-ontogenetic 'noise' superimposed over ontogenetic variability may be responsible for the trend evident in *A. abbreviatus* and the lack of trend in *A. prattii*.

Comparison between individuals in a population is useful in discounting the possibility of ontogenetic shortening of stems by resorption of stereom more or less equally from each columnal (as opposed to resorption of the distalmost columnal only). Individuals have short stems because they have few columnals not because they have columnals of lesser height.

Conclusion

The dynamics of stem ontogeny in *Ailsacrinus* are equivocal. The presence of lenticular columnals in some stems cannot be taken as evidence for addition of columnals; proximal–distal gradients of columnal size-change are variable and can be interpreted in more than one way; distal columnals with exposed symplectial facets in *A. abbreviatus* might indicate some shedding of columnals; and crinoid size : column length comparisons within populations suggest post-detachment net addition of columnals in *A. abbreviatus* but not in *A. prattii*.

Palaeoecology

Broad environment

The Middle Jurassic sediments of southern England are predominantly carbonates. They accumulated in a shallow shelf sea where conditions were influenced by the presence of the London–Belgian Island in the east, a probable source of fresh water and terrigenous clastic material (see Ware & Windle 1981). Comparatively open, marine-shelf environments existed in the south and west during the Bathonian (for example, around Bath). Environments of the Northleach area may have often been more stressful for marine biota as a result of closer proximity to land (see Palmer 1979).

Sellwood & McKerrow (1974) discussed the stratigraphy and depositional environments of the lower part of the Bathonian in Oxfordshire and north Gloucestershire including the Northleach region. They recognized three stratigraphical divisions: Chipping Norton Formation, overlain by Sharps Hill Formation and then Taynton Limestone Formation. The fauna of the Sharps Hill Formation, in which *A. abbreviatus* probably occurs, is predominantly marine, although the presence of *Liostrea* life assemblages may indicate some salinity restriction (as, for example, some of the present day Florida Keys). Water depth is believed to have been little more than 3 m. The Sharps Hill Formation appears to grade laterally into the upper part of the Lower Fullers Earth Formation which is well-developed further south and west. This led Sellwood & McKerrow (1974) to ascribe deposition of the Sharps Hill Formation to a minor transgression which caused deeper-water sediments of Lower Fullers Earth Formation lithology to spread onto the carbonate-dominated area of north Gloucestershire and Oxfordshire.

Green & Donovan (1969) described the Great Oolite of the Bath region but did not deal with outliers north of the River Avon such as Lansdown Hill. They divided the Great Oolite sequence, from bottom to top, into Combe Down Oolite, Twinhoe Beds, Bath Oolite and Upper Rags. It is not known where the Lansdown *A. prattii* locality fits within this succession. The Bath area was apparently located on the outer part of a stable carbonate shelf. The Combe Down Oolite is interpreted as a shallow-water deposit formed by oolite deltas which flanked tidal flats with migrating channels (like the present day Trucial Coast). While the succeeding

Twinhoe Beds may have been deposited in quieter and rather deeper water, the Bath Oolite seems to make a return to conditions similar to those inferred for the Combe Down Oolite. The Upper Rags may represent a more varied depositional regime. Analysis of a single bed exposed on Bathampton Down (Elliott 1974) suggests that it accumulated on a current-swept, inter-reef seafloor like some modern environments which exist in water 30–60 m deep off the Capricorn Islands (Great Barrier Reef) and the Bermudas.

The Eastington crinoid bed
A detailed study has been undertaken of the *A. abbreviatus* bed from the new locality near Eastington. Within the confines imposed by poor exposure, this has allowed a tentative model to be proposed for the genesis of the Eastington crinoid bed incorporating sedimentological, palaeoecological and taphonomic inferences.

LITHOLOGY. The well-sorted bio-oosparite (Fig. 3, p. 41) comprising the bulk of the bed is clean-washed and was undoubtedly formed, although not necessarily deposited, in a comparatively agitated environment. Features indicating a storm deposit ('tempestite' of Ager, 1974), such as matrix-supported intraclasts, are notably absent. The subparallel orientation of shell fragments (Fig. 3A) suggests grain by grain deposition rather than the nearly instantaneous deposition caused by a storm. The thin muddy layers which drape each fossiliferous bedding plane stand in marked contrast to the bio-oosparite. The major clay mineral present in this mud is illite; there are no clay minerals which may be interpreted as having a volcanogenic origin. This is important because elsewhere in the British Jurassic, Ali (1977) has postulated smothering by volcanic ash as a source of catastrophic mortality of corals. Survival of discrete muddy layers without mixing with the clean-washed carbonate sediment suggests that the mud was stabilized during carbonate deposition. Stabilization of mud in Recent sedimentary environments is commonly achieved by the presence of an algal mat or other organic film (e.g. Bathurst 1975: 122).

SEDIMENTARY STRUCTURES. Bioturbation is absent from the crinoid bed and this is true for the Sharps Hill Formation in general (Sellwood & McKerrow 1974). Burrowing animals, whose activities would probably have disarticulated the buried crinoids, may have been excluded by rapid deposition (Sellwood & McKerrow 1974) or by unfavourable anaerobic conditions beneath the sediment surface (cf. Rosenkranz 1971). The existence of anaerobic conditions is supported by apparent pigment preservation in *A. abbreviatus*; Blumer (1960) ascribes preservation of organic pigments in fossil crinoids to the presence of strongly reducing conditions. This in turn is consistent with the possibility of an organic film stabilizing the muddy sediment.

Traces of symmetrical ripples occur near the top of the crinoid bed. These wave-generated bedforms would have been produced in shallow water above wave base.

CRINOID PRESERVATION. Most specimens of *A. abbreviatus* are exceptionally well preserved, lacking post-mortem abrasion and with delicate structures (e.g. pinnule cover plates) usually intact and unbroken. The crinoids are well-articulated, especially near the base of the bed. The overlying shell lag deposit contains short, articulated fragments, possibly reworked from the crinoid bed below. Where arms are disarticulated, the amount of dislocation between the disarticulated portions tends to be small. Similar preservation in other fossil crinoids is generally attributed to rapid burial *in situ* or with very minor transportation (e.g. Brett 1978, Brower 1973, Hess 1972, 1973). Aslin (1968) also suggests rapid burial to account for good preservation of echinoids in rocks of Middle Jurassic age in Northamptonshire. Working with living crinoids, Cain (1968: 192) found that, within two days of death, specimens of *Antedon bifida* in still water 'collapsed into a mass of arms and cirrus fragments'. Similarly, comatulids studied by Liddell (1975) were completely disarticulated within two days of death when placed in an agitated environment but crinoids buried and then exhumed after six days were well-preserved and retained their colour. However, considerable interspecific variation in the disarticulation rates of Recent crinoids and ophiuroids was found by Meyer (1971). Scavenging organisms played an important role in the disarticulation process. These studies on living crinoids provide strong
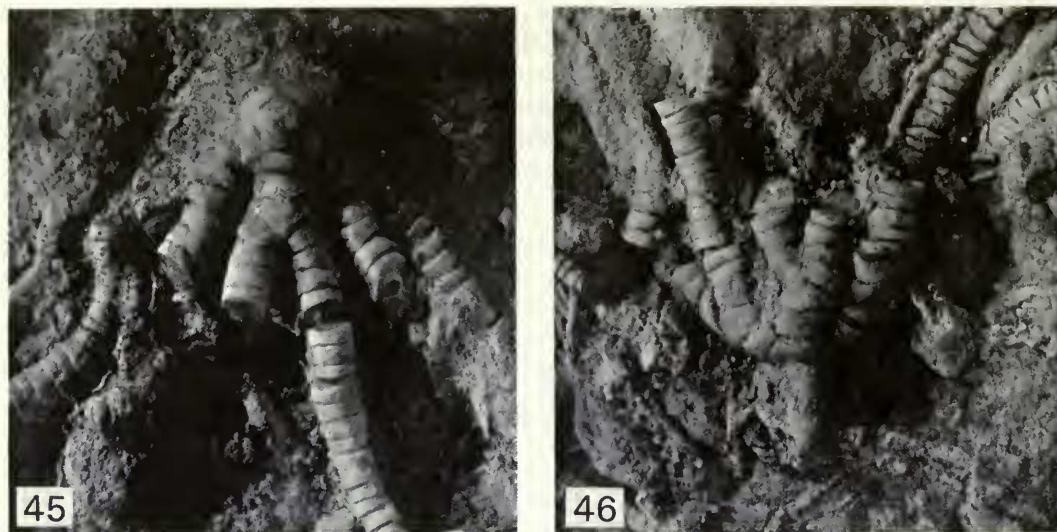
Figs 45–46 *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington.
Fig. 45, BMNH E67807, short-stemmed crinoid in an upright orientation on the underside of a
bedding plane; × 2·3. Fig. 46, BMNH E67817, long-stemmed crinoid lying prostrate on a bedding
plane; × 1·9.

evidence for rapid burial of individuals of *A. abbreviatus*. This probably occurred while the
crinoids were still alive or, less likely, shortly after death. Transport of dead crinoids over
significant distances can be discounted but it is possible that they were swept to their burial site
before death.

CRINOID ORIENTATION. Over 50% of the crinoids studied are preserved in presumed life-position,
i.e. with their adoral surfaces facing upwards. In these individuals the arms diverge radially from
the cup (Fig. 25, p. 52) and lie parallel or almost parallel to the bedding. The short stem is
orientated perpendicular to the bedding (Fig. 45). About 40% of the crinoids are prostrate,
typically with arms close together and arms and stem parallel or subparallel to the bedding (Fig.
46). Some individuals are obliquely orientated and a few are upside down. There is no
discernible alignment of prostrate crinoids or groups of arms on the bedding planes. Tangling of
arms is rare despite high concentrations of specimens. Many arms are bent, flexed either
aborally or adorally. Some bent arms extend upwards through a few centimetres of sediment.

This orientational evidence shows that at least some of the crinoids were disturbed from their
presumed life positions before or during burial. The arms of partially buried crinoids are
unlikely to have projected above the sea-bed for very long before disarticulating. The occur-
rence of arms orientated at high angles to the bedding thus again suggests rapid deposition, and
their lack of alignment that the crinoids were not buried in a regime of strongly directional
currents.

POPULATION DENSITY. The mud-draped bedding planes are characterized by a high density of
crinoids, exceeding 200/m² in some instances. High population density may be attributed to
concentration by currents or burial of a densely aggregated living population. Dense aggre-
gations of fossil crinoids, so-called 'crinoid gardens' (Moore & Teichert *in* Ubaghs *et al.* 1978:
T8), are well known among pelmatozoic species (e.g. Brower 1973, Brett 1978). Highly
aggregated populations are also a feature of some Recent comatulids (see Reese 1966; Breimer
in Ubaghs *et al.* 1978: T328); Marr (1963) for example illustrates an Antarctic sea-bed densely
colonized by comatulids. According to Keegan (1974), *Antedon bifida* may achieve population
densities of 1200/m² on the west coast of Ireland. Aggregation may arise from poor larval
dispersal, selection of favourable habitats already populated by conspecifics, or truly gregarious

behaviour (preferential settlement of larvae close to conspecifics). The advantages of aggregation have been considered by Warner (1971, 1979). He notes that it is likely to promote cross-fertilization, increase stability in current-swept areas, allow the mutual support of arms raised in suspension feeding and enhance settlement of food particles from suspension because a mass of individuals forms an effective current baffle. Wilson, Holme & Barratt (1977) suggest protection from predation as a further advantage of aggregation in echinoderms. It is difficult to discount conclusively concentration by currents as the cause of high population density in *A. abbreviatus*, but the alternative hypothesis of burial of an aggregated living population is more appealing in view of the analogues which exist among comatulids at the present day.

POPULATION VARIABILITY AND STRUCTURE. Variation in axillary brachial height, used as a convenient indicator of crinoid size (see p. 62), shows the variability of *A. abbreviatus* in the Eastington crinoid bed (Fig. 47). A sample of 128 crinoids derived from various parts of the bed has a size frequency distribution which is almost normal. In contrast, a subsample of 37 crinoids on a single bedding plane has a negatively skewed distribution. Interpretation of these patterns of distribution can be made either on the premise that they show variation within a population of
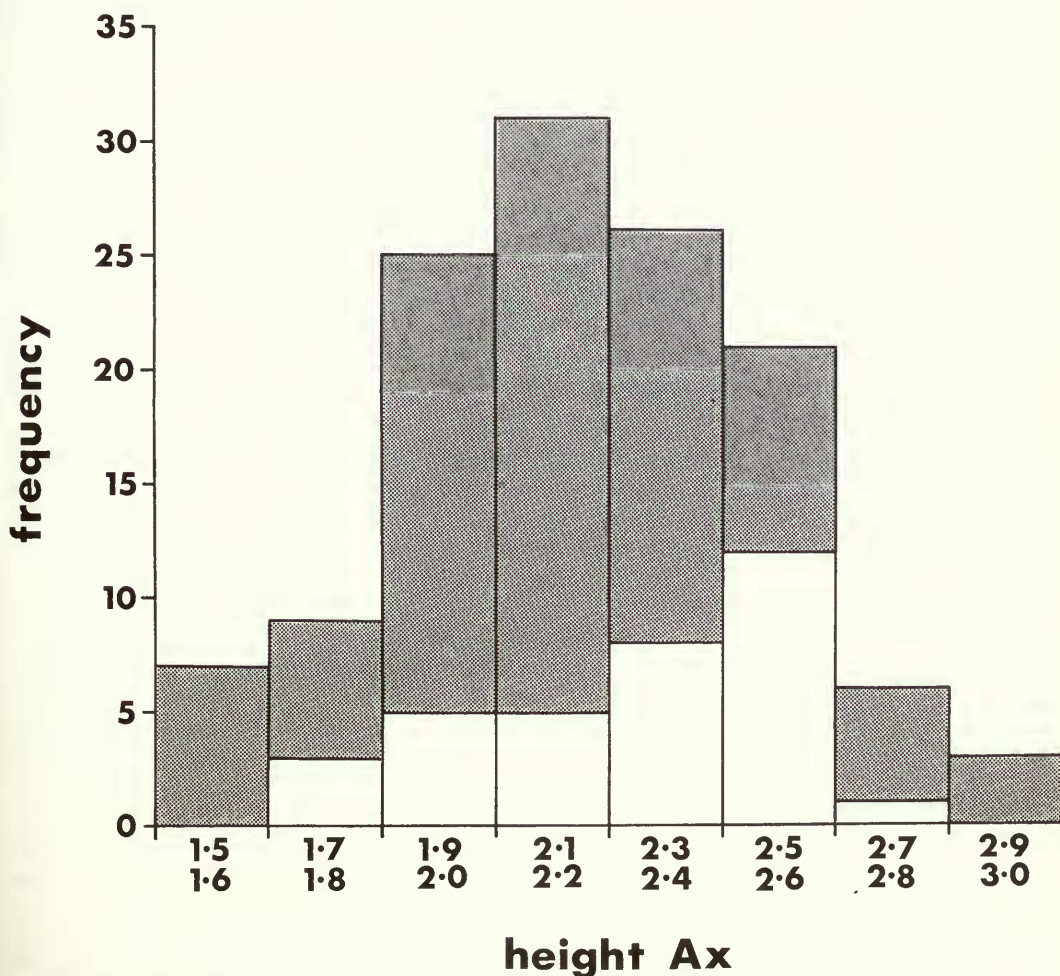
Fig. 47   Frequency histogram of crinoid size (expressed as height of the axillary brachial in mm) in 128 individuals of *Ailsacrinus abbreviatus* gen. et sp. nov. from the Bathonian (? Sharps Hill Fm.) of Eastington. A subsample of 37 individuals from a single bedding plane is unshaded.

equal-aged individuals, or that size reflects age and the distribution reveals the demographic structure of the crinoid population. In reality, the distribution is likely to be the result of a combination of these non-ontogenetic and ontogenetic factors. However, for present purposes it will be assumed that ontogenetic factors predominate and the data will be analysed accordingly.

Hallam (1972) reviewed the interpretation of population structure in fossils. He distinguished between living populations and death assemblages, each of which is likely to produce a different type of size frequency distribution. The size frequency histogram for a living population is very often polymodal because recruitment to the population tends to be episodic (e.g. seasonal), giving distinct age/size classes. For death assemblages a unimodal distribution is more probable and the shape of the distribution is dependent largely on rates of growth and mortality. Benthic assemblages usually have positively skewed distributions due to high juvenile mortality, while normal distributions are unusual, and negatively skewed distributions highly exceptional.

The size frequency distribution of *A. abbreviatus* fits neither that typical of a living population (though population structure in crinoids specifically may be unknown) nor that typical of a death assemblage. If the model proposed below for the formation of the Eastington crinoid bed is correct, then the crinoids represent a succession of living populations which were catastrophically buried. The size frequency distribution of the large sample of crinoids from throughout the bed may be a mixture of several living populations. However, that of crinoids on a single bedding plane could reflect the structure of a single population. This is a negatively skewed distribution; large, presumed old, individuals are over-represented. Such a population structure is consistent with continuous recruitment of adult crinoids into the population following a period of attached life elsewhere. Assuming growth rate to have decreased during ontogeny, the proportion of large crinoids in the population would increase with time, yielding a negatively skewed size frequency histogram.

TENTATIVE MODEL OF CRINOID BED FORMATION. Evidence for rapid sediment-deposition and disturbed crinoid burial seems clear. The sediment responsible for crinoid burial appears to have been the clean-washed carbonate sand rather than the mud of the bedding-plane drapes. Significant transport of crinoids before burial is thought unlikely and sediment inundation of densely-aggregated living populations *in situ* or very locally transported seems more probable. A multi-event model seems more compatible with the evidence than a single event model. This model can be summarized as follows:

1. Colonization of the sea-bed by crinoids and deposition of muddy sediment in fairly quiet water aided by the baffling action of the crinoid arms. Once deposited, the mud may have been stabilized by an organic film which also promoted anaerobic conditions within the sediment and precluded infauna whose activities may otherwise have disarticulated crinoids already buried. Adult crinoids were recruited into the densely aggregated crinoid population by migration from sites of attachment located elsewhere.

2. Rapid influx of clean-washed carbonate sand generated in a higher energy environment and possibly introduced by tidal currents. Some of the crinoids were buried immediately and retained their upright life-orientation, but others were disturbed from their life-orientation, locally transported, and buried prostrate or upside down.

3. Return to normal conditions with recolonization by crinoids and recommencement of mud sedimentation.

4. Repetition of this sequence of events to give the full thickness of the crinoid bed.

5. Change in the sedimentary regime signalled by the deposition of a cross-bedded shell lag over the crinoid bed, perhaps due to the advance of a dune field.

Stem function

Inference of stem function is important in understanding the mode of life of *Ailsacrinus*. As there are no living crinoids of known ecology which have a stem morphology similar to that of *Ailsacrinus*, a functional morphological approach has been applied to the problem of stem function (Rudwick 1961).

Potential functions of the stem in *Ailsacrinus* are:

1. as a column to hold the crown aloft;
2. as a means of attaching the crinoid to the substrate;
3. as ballast to stabilize the crinoid;
4. as a counterpoise to keep the crinoid in an appropriate orientation; or
5. without function, at least during the unattached period of life.

COLUMN. The paradigm for a column functioning to elevate the crown is a stout structure with little flexibility between columnals, thickened at its base where stresses caused by horizontal water-movements could be concentrated, and flat-bottomed or firmly attached to the substrate by some means. This paradigm, approached in articulates such as *Apiocrinites* (Breimer & Lane in Ubaghs *et al*. 1978: T334), is clearly not fulfilled by *Ailsacrinus*.

ATTACHMENT. Attachment structures or holdfasts are part of the fossilizable skeleton in various crinoids. Alternative but equally viable solutions to anchoring the crinoid are provided by different types of holdfast fitted to soft substrates, hard bottoms, substrates with a complex relief, etc. (see Brett 1981). Paradigms for attachment generally involve structures of expanded surface area (e.g. cemented bases or divided distal ends of the stem) and/or with the ability to grasp (e.g. comatulid cirri). It seems clear that the stem of *Ailsacrinus* lacked any adaptation for attaching the crinoid.

BALLAST. The function is fulfilled by any structure denser than sea-water. The optimal weight of ballast required might be expected to vary according to the unknown factors of net crinoid buoyancy and strength of environmental water currents. Therefore, it is difficult to assess the possible role as ballast of the stem in *Ailsacrinus*.

COUNTERPOISE. The paradigm for a counterpoise structure providing stability has a low centre of gravity close to the substrate. This is well illustrated by the stemless inadunates *Agassizocrinus* (Ettensohn 1975) and *Paragassizocrinus* (Ettensohn 1980), which have heavily-calcified infrabasal cones giving them a 'roly-poly doll' construction. The counterpoise paradigm may be approached adequately in some very short-stemmed individuals of *Ailsacrinus* but it is certainly not fulfilled in long-stemmed individuals of *A. prattii* where the centre of gravity is likely to have been located in the proximal part of the stem some way above the substrate.

FUNCTIONLESS. To argue effectively that a structure is functionless it is necessary to eliminate all possible functions. This is clearly impossible if only for the reason that not every function may have been conceived. However, a hypothesis which deserves consideration for *Ailsacrinus* is that the stem was functional (e.g. for attachment and crown elevation) during the attached stage of ontogeny but essentially functionless when the free-living stage was reached. In Recent isocrinids (Rasmussen 1977) the long cirriferous stem may fracture at the cryptosymplexy beneath a nodal, leaving the crown and proximal part of the stem to drift away before becoming re-attached elsewhere. Stem fracturing may represent true autotomy or, as believed by Rasmussen, breakage in response to water movements or other external forces. A similar process of stem fracturing, but without subsequent cirral reattachment, may be envisaged for *Ailsacrinus*, perhaps at a late stage in ontogeny (see above). If caused by external pressure, stem breakage may have left individuals with stems of widely varying length. Thereafter, individuals possibly lacked the ability to shorten the stem and relied on occasional accidental shedding of columnals.

Feeding ecology

Present interest in the feeding ecology of living and fossil crinoids focuses on an apparent polarization into current-seeking rheophiles and current-avoiding rheophobes (Breimer 1969, Breimer & Lane *in* Ubaghs *et al*. 1978: T333). Rheophiles, present among Recent stalked crinoids and comatulids, commonly form brachial filtration fans (Magnus 1967). The arms are spread in a paraboloid with their adoral surfaces pointing upcurrent. A radial feeding posture is less common. Rheophobes, possibly a minority of living crinoids, include deep water comatulids

(Pérès 1958, 1959) in which the arms form a collecting bowl for feeding on the plankton rain. However, there may be considerable variation in feeding behaviour within some species and the ecological dichotomy into rheophiles and rheophobes may break down. For example, La Touche (1978) observed that flexibility in the arm movements of *Antedon bifida* allowed individuals to feed in diverse current regimes. In slack water, animals most commonly held their arms in an inverted cone. Animals in current speed of up to 30 cm/s held their arms in the shape of a bent-over, flattened cone.

Breimer & Lane (*in* Ubaghs *et al*. 1978) discuss features of the stalk and arms useful as a guide to inferring the palaeoecology of fossil crinoids. Species of *Millericrinus* with a rudimentary stem (evidently referring to *Ailsacrinus*) they consider (1978: T334) to be benthic rheophobes. Certainly it is difficult to envisage *Ailsacrinus* forming a radial brachial filtration fan for rheophilic feeding; the stem is not long enough to hold the crown high enough aloft. The lack of anchorage structures seems to be another problem. Individuals lack grasping cirri and also hooks or spines on the arms and pinnules which are used for attachment in some comatulids (e.g. *Comanthina schlegeli*) that secondarily lose their cirri (Meyer & Macurda 1977). However, not all rheophiles form brachial filtration fans and, if *Ailsacrinus* lived in dense populations, stability may not have necessitated direct attachment to the substrate. Ecological analogies may be valid with the living brittle star *Ophiothrix fragilis* (see Warner 1979). Like *Ailsacrinus*, *O. fragilis* is a suspension feeding echinoderm living in dense aggregations composed of individuals lacking a means of direct attachment to the sea bed. Arms of individuals are stretched upwards into the current and interlock to form a mat stable in velocities exceeding 20 cm/s. Aggregations are probably maintained by preferential settlement of larvae around adults, combined with the ability of dislodged adults to locate aggregations and walk towards them.

To summarize, *Ailsacrinus* may have been either a rheophobic or rheophilic suspension feeder living in dense populations. Recruitment into these crinoid mats seems to have taken place by immigration of individuals which had attained an adult size during a protracted period of attached ontogeny spent elsewhere. The active locomotory abilities of *Ailsacrinus* were perhaps limited; arms are robust and muscular fossae small. Migration was more likely achieved by passive drifting or comasterid-like crawling than by antedonid-like swimming. This ecological model, devised largely using evidence from *A. abbreviatus*, may or may not apply to *A. prattii*.

Evolution

Phylogenetic affinities

The Articulata are divided into seven orders by Ubaghs (*in* Ubaghs *et al*. 1978: T364): Millericrinida, Cyrtocrinida, Bourgueticrinida, Isocrinida, Comatulida, Uintacrinida and Roveacrinida. Evolutionary relationships between these orders are poorly understood (see Rasmussen *in* Ubaghs *et al*. 1978: T302–5; Pisera & Dzik 1979). Although articulate crinoids are usually considered to have evolved from the Poteriocrinina, a group of dicyclic Palaeozoic inadunates, their structural diversity is taken by some to suggest a polyphyletic origin (Ubaghs *in* Ubaghs *et al*. 1978: T281).

Cyrtocrinids, bourgueticrinids, uintacrinids and roveacrinids are well-defined and morphologically distinctive groups which can be eliminated from any discussion of the affinities of *Ailsacrinus*. This leaves the millericrinids, isocrinids and comatulids, all of which are known in deposits of Bathonian age. Millericrinids are characterized by the presence of a proximale and a lack of cirri. The column typically forms a conical transition to the cup. Nodals are absent, although the alternately large and small columnals in *Angulocrinus* (Rasmussen *in* Ubaghs *et al*. 1978: fig. 550,2) resemble nodals and internodals respectively. Isocrinids possess nodals and cirri but lack a proximale. Comatulids have a reduced stem consisting of a single cirriferous centrodorsal or, in early forms, a few reduced nodals (Hess 1951). Previously, *Ailsacrinus* (as *Millericrinus prattii*) has been assigned to the millericrinids.

Table 1 summarizes the principal morphological characters shared by *Ailsacrinus* with typical millericrinids, isocrinids and comatulids. These characters are discussed in turn below.

Table 1 Morphological characters shared by *Ailsacrinus* with Millericrinida, Isocrinida and Comatulida.

	Ailsacrinus	Millericrinida	Isocrinida	Comatulida
Stem	reduced	large	large	reduced
Proximal columnal	fused	fused	free	fused
Cirri	absent	absent	present	present
Basals	reduced	large	reduced	reduced
Oral pinnules	present	absent	absent	present
Syzygies	present	absent?	present	present

STEM. A reduced stem, shared by *Ailsacrinus* and comatulids, is presumably an advanced character but is not a reliable synapomorphy because stem reduction has undoubtedly occurred several times during crinoid evolution (see Kirk 1911). Furthermore, reduction of the stem to a single centrodorsal in comatulids seems to have been the result of columnal fusion, a process for which there is no evidence in *Ailsacrinus*.

PROXIMAL COLUMNAL. A fused proximal columnal is present as a proximale in *Ailsacrinus* and millericrinids, and as a centrodorsal in comatulids. Although fusion may be an advanced character and is absent in isocrinids, homology between the proximale of *Ailsacrinus* and the centrodorsal of comatulids is unlikely because the former is united to the cup by a symplectial articulation and the latter by a synostosial articulation.

CIRRI. By outgroup comparison with poteriocrininids, cirri may be a primitive character of the Articulata. If so, absence of cirri is an advanced character shared by *Ailsacrinus* and millericrinids. Character absences may, however, be unreliable indicators of phylogenetic affinity.

BASALS. Reduced basals are shared by *Ailsacrinus*, isocrinids and comatulids. Despite the fact that small basals may be an advanced character state (by outgroup comparison), basal reduction is a comparatively simple process with a high probability of occurring more than once. If so, reduced basals are not a good synapomorphy.

ORAL PINNULES. Among living crinoids, oral pinnules are said to be restricted to comatulids (Breimer *in* Ubaghs *et al*. 1978: T43). They appear not to have been described from non-comatulid articulates prior to this account of *Ailsacrinus*. The fine structure of oral pinnules in *Ailsacrinus* differs somewhat from those of comatulids. Oral pinnules of the antedonid *Promachocrinus* are slender, with long, elongate pinnulars (Breimer *in* Ubaghs *et al*. 1978: fig. 28,4), whereas those of comasterids possess distinctive distal pinnulars equipped with teeth to form terminal combs (Breimer *in* Ubaghs *et al*. 1978: fig. 28,3). In *Ailsacrinus* the pinnulars are short and high, and lack terminal combs. The phylogenetic significance of oral pinnules in *Ailsacrinus* is difficult to assess because of this disparity in detailed structure, and because oral pinnules may be present in other fossil millericrinids but have not been recognized owing to inferior preservation. The extant millericrinid suborder Hyocrinina provides no help in resolving this problem because these living crinoids are devoid of pinnules on their proximal brachials.

SYZYGIES. Syzygies are well-developed in *Ailsacrinus* and, as in comatulids, the hypozygals lack pinnules. The frequency of syzygies along the arms of *Ailsacrinus* is similar to that of comatulids. However, the first syzygy in *Ailsacrinus* occurs between secundibrachs 4 and 5 whereas the usual position for this ligamentary articulation in comatulids is between secundibrachs 3 and 4. There are clear differences in stereom ultrastructure between the syzygial facets of *Ailsacrinus* and comatulids, those of *Ailsacrinus* having a subconcentric fascicular fabric. Although Rasmussen (*in* Ubaghs *et al*. 1978: T817) states that syzygies are absent in millericrinids, facets of disarticulated brachials from another millericrinid, *Apiocrinites*, often bear a pattern of radiating ridges suggestive of a syzygial articulation. Furthermore, the occurrence of
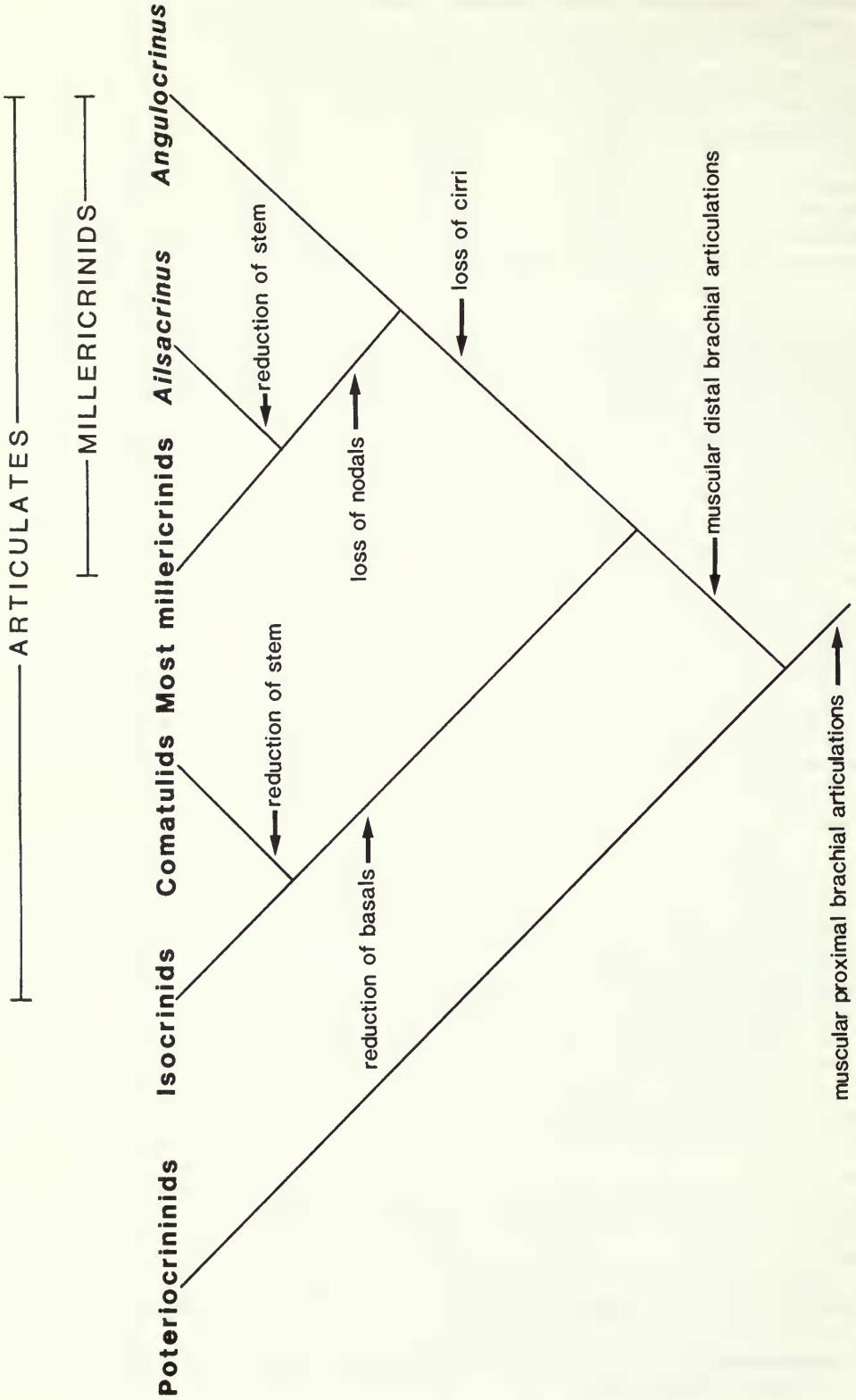
Fig. 48 Tentative cladogram showing inferred relationships between *Ailsacrinus* gen. nov. and some other crinoids.

possible syzygies in certain poteriocrininids (Strimple *in* Ubaghs *et al*. 1978: T301) suggests that they may be a primitive character of articulate crinoids and of no value in deciding relationships in the group.

The foregoing discussion serves to highlight the acute need for more information on the morphology of articulates, especially their brachial articulations and pinnule structure. Until this is forthcoming, relationships within the group will remain obscure. Therefore the favoured cladogram (Fig. 48) showing the relationships between *Ailsacrinus* and other articulates is very tentative. *Ailsacrinus* is here interpreted as a millericrinid possessing autapomorphies (reduced stem and basals, oral pinnules, well-developed syzygies) resulting in a morphology convergent with comatulids.

Adaptive evolution

When discussing the post-Palaeozoic evolution of crinoids, Meyer & Macurda (1977) focused on the impressive adaptive radiation shown by the Comatulida. They considered articulates to be pre-adapted for an eleutherozoic existence because they possess muscular arms which are potentially of value in crawling and swimming, as in comatulids. Active locomotion is used by comatulids to seek favourable habitats and to avoid stress. Meyer & Macurda (1977) identified predator stress, imposed by diversifying teleost fish, as an important selective factor during comatulid evolution.

In view of the similar time of origin of comatulids (known from the Toarcian) and *Ailsacrinus*, it is tempting to explain the origin of *Ailsacrinus* in identical terms. However, eleutherozoic lifestyles may have characterized many other extinct crinoids and seem to have arisen several times among Palaeozoic taxa. These Palaeozoic crinoids were neither pre-adapted in the sense of having muscular arms nor subjected to the predator stress of teleosts. The origin of both comatulids and *Ailsacrinus* in Jurassic times may be quite coincidental.

Temporal trends of morphological change apparent within the genus *Ailsacrinus* are the opposite of those expected. The older species, *A. abbreviatus*, resembles less the putative stalked ancestor of the genus than does the later *A. prattii*, which usually has a longer stem and altogether more bulky morphology. Early notions of *Ailsacrinus* were of a crinoid evolving towards a fully eleutherozoic lifestyle by elimination of the stem. The modest evidence from the two known species fails to support this hypothesis.

Of *Millericrinus prattii*, Kirk (1911: 49) said '. . . were *Millericrinus* to have possessed cirri, there is small doubt that this very species would have formed the radicle of a line essentially comatulid in habit, and perhaps of considerable vigor.' This viewpoint remains an appropriate epitaph for an ecological excursion by the millericrinids into an eleutherozoic lifestyle which proved unsuccessful in terms of duration and taxonomic fecundity.

Acknowledgements

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